A TEXT-BOOK

OF

HUMAN PHYSIOLOGY;

DESIGNED FOR THE USE OF

PRACTITIONERS AND STUDENTS OF MEDICINE.

BY

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ILLUSTRATED BY THREE LITHOGRAPHIC PLATES AND THREE HUNDRED AND THIRTEEN WOODCUTS.

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PREFACE.

IN preparing this text-book for the use of students and practitioners of medicine, I have endeavored to adapt it to the wants of the profession, as they have appeared to me after a considerable experience as a public teacher of human physiology. My large treatise in five volumes is here condensed, and I have omitted bibliographical citations and matters of purely historical interest. Many subjects, which were considered rather elaborately in my larger work, are here presented in a much more concise form. I have added, also, numerous illustrations, which I hope may lighten the labors of the student. A few of these are original, but by far the greatest part has been selected from reliable authorities. I have thought it not without historical interest to reproduce exactly some of the classical engravings from the works of great discoverers, such as illustrations contained in the original editions of Fabricius, Harvey, and Asellius. In addition, I have reproduced a few of the beautiful microscopical photographs taken at the United States Army Medical Museum, under the direction of Dr. J. J. Woodward, to whom I here express my grateful acknowledgments. I have also to thank M. Sappey for his kindness in furnishing electrotypes of many of the superb engravings with which his great work upon anatomy is illustrated.

My work in five volumes was intended as a book of reference, which I hope will continue to be useful to those who desire an account of the literature of physiology, as well as a statement of the facts of the science. I have always endeavored, in public teaching, to avoid giving undue prominence to points in which I might myself be particularly interested, from having made them subjects of special study or of original research. In my text-book, I have carried out the same idea, striving to teach, systematically and with uniform emphasis, what students of medicine are expected to learn in physiology, and avoiding elaborate discussions of subjects not directly connected with practical medicine, surgery, and obstetrics. While I have referred to my original observations upon the location of the sense of want of air in the general system, the new excretory function of the liver, the function of glycogenesis, the influence of muscular exercise upon the elimination of urea, etc., I have not considered these subjects with great minuteness and have generally referred the reader to monographs for the details of my experiments.

Finally, in presenting this work to the medical profession, I cannot refrain from an expression of my acknowledgments to the publishers, who have spared nothing in carrying out my views and have devoted special pains to the mechanical execution of the illustrations.

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CONTENTS.

CHAPTER V.

CHANGES WHICH THE AIR AND THE BLOOD UNDERGO IN RESPIRATION.

CHAPTER VI.

ALIMENTATION.

CHAPTER VII.

DIGESTION, MASTICATION, INSALIVATION, AND DEGLUTITION.

CHAPTER VIII.

STOMACH-DIGESTION.

CHAPTER IX.

INTESTINAL DIGESTION—DEFÆCATION.

CHAPTER X.

ABSORPTION—LYMPH AND CHYLE.

CHAPTER XI.

SECRETION.

CHAPTER XII.

EXCRETION BY THE SKIN AND KIDNEYS

CHAPTER XIII.

FUNCTIONS OF THE LIVER.

CHAPTER XIV.

THE DUCTLESS GLANDS.

CHAPTER XV.

NUTRITION—ANIMAL HEAT.

CHAPTER XVI.

MOVEMENTS—VOICE AND SPEECH.

CHAPTER XVII.

PHYSIOLOGICAL DIVISIONS, STRUCTURE, AND GENERAL PROPERTIES OF THE NERVOUS SYSTEM.

CHAPTER XVIII.

SPINAL NERVES—MOTOR CRANIAL NERVES.

CHAPTER XIX.

SENSORY CRANIAL NERVES.

CONTENTS.

CHAPTER XX.

FUNCTIONS OF THE SPINAL CORD.

CHAPTER XXI.

THE ENCEPHALIC GANGLIA.

CHAPTER XXII.

SYMPATHETIC NERVOUS SYSTEM—SLEEP.

CHAPTER XXIII.

SPECIAL SENSES—TOUCH, OLFACTION, AND GUSTATION.

CHAPTER XXIV.

VISION.

CHAPTER XXV.

AUDITION.

CHAPTER XXVI.

ORGANS AND ELEMENTS OF GENERATION.

CHAPTER XXVII.

FECUNDATION AND DEVELOPMENT OF THE OVUM.

CHAPTER XXVIII.

FŒTAL LIFE—DEVELOPMENT AFTER BIRTH—DEATH.

LIST OF ILLUSTRATIONS.

HUMAN PHYSIOLOGY.

CHAPTER I.

THE BLOOD.

General considerations—Transfusion—Quantity of blood—General characters of the blood—Blood-corpuscles—Development of the blood-corpuscles—Leucocytes—Development of leucocytes—Composition of the red corpuscles—Globuline—Hæmaglobine—Analysis of the blood—Composition of the blood-plasma—Inorganic principles—Organic saline principles—Organic non-nitrogenized principles—Excrementitious matters—Organic nitrogenized principles—Plasmine, fibrin, metalbumen, and serine—Peptones—Coloring matter—Coagulation of the blood—Characters of the clot—Characters of the serum—Circumstances which modify coagulation—Coagulation of the blood in the organism—Spontaneous arrest of hæmorrhage—Cause of the coagulation of the blood—So-called fibrin-factors—Paraglobuline, or fibrinoplastic matter—Fibrinogen.

From the earliest periods in the history of physiology, the importance of the blood has been recognized; and, with the progress of knowledge, this great nutritive fluid has been shown to be more and more intimately connected with the phenomena of animal life. It is now known to be the most abundant and highly organized of the fluids of the body, providing materials for the regeneration of all parts, without exception, receiving the products of their waste and conveying them to proper organs, by which they are removed from the system. These processes require, on the one hand, constant regeneration of the nutritive constituents of the blood, and, on the other, its constant purification by the removal of effete matters.

Those tissues in which the processes of nutrition are active are supplied with blood by vessels; but some, less highly organized, like the epidermis, hair, cartilage, etc., which are called extra-vascular because they are not penetrated by vessels, are none the less dependent upon the blood, as they imbibe nutritive material from the blood of adjacent parts.

The importance of the blood in the processes of nutrition is evident; and, in animals in which nutrition is active, death is the immediate result of its abstraction in large quantity. Its importance to life can be readily demonstrated by experiments upon the inferior animals. If we take a small dog, introduce a canula through the right jugular vein into the right side of the heart, adapt to it a syringe, and suddenly withdraw a great part of the blood from the circulation, immediate suspension of all the so-called vital processes is the result. If we then return the blood to the system, the animal is as suddenly revived. To perform this experiment satisfactorily, we must accurately adjust the capacity of the syringe to the size of the animal.

Certain causes, one of which is diminution in the force of the heart's action after copious hæmorrhage, prevent the escape of all the blood from the body, even after division of the largest arteries; but, after the arrest of the functions which follows copious discharges of this fluid, life may be restored by injecting into the vessels the same blood or the fresh blood of another animal. This observation, which was first made on the inferior animals, has been applied to the human subject; and it has been ascertained that, in patients sinking under hæmorrhage, the introduction of even a few ounces of fresh blood may restore the functions for a time, and sometimes permanently. The operation of transfusion, which consists in the introduction of the blood of one individual into the vessels of another, was performed upon animals in the middle of the seventeenth century, and was soon after attempted in the human subject. So great was the enthusiasm with which some regarded these experiments, that it was thought possible even to effect a renewal of youth by the introduction of young blood into the veins of old persons; and it was also proposed to cure certain diseases, such as insanity, by actual renewal of the circulating fluid. These ideas were not without apparent foundation. It was stated, in 1667, that a dog, old and deaf, had his hearing improved and was apparently rejuvenated by transfusion of blood from a young animal. A year later, Denys and Emmerets published a case of a maniac who was restored to health by the transfusion of eight ounces of blood from a calf; and another case was reported of a man who was cured of leprosy by the same means. But the case of insanity, which was apparently cured, suffered a relapse, and the patient died during a third attempt at transfusion. It is almost unnecessary to say that these extravagant expectations were not realized. In fact, some operations were followed by such disastrous consequences, that the practice was forbidden by law in Paris in 1668, and soon fell into disuse.

Transfusion, with more reasonable applications, was revived in the early part of this century (1818) by Blundell, who, with others, demonstrated its occasional efficacy in desperate hæmorrhage and in the last stages of some diseases, especially cholera. There are now quite a number of cases on record where life has been saved by this means; and oftentimes, when the result has not been so happy, the fatal event has been considerably delayed.

Numerous experiments on transfusion in animals have been performed, with very interesting results. Prévost and Dumas have shown that, while an animal may be restored after hæmorrhage by the transfusion of defibrinated blood, no such effect follows the introduction of the serum; showing that the vivifying influence in all probability resides in the corpuscles. Brown-Séquard has shown that, in parts detached from the body, after nervous and muscular irritability have disappeared, these properties may be restored for a time by the injection of fresh blood. He also made a curious experiment in which blood was passed from a living dog into the carotid of a dog just dead from peritonitis. The animal was so far revived by this operation as to sustain himself on his feet, wag his tail, etc., and died a second time, twelve and a half hours after. In this experiment, insufflation was employed in addition to the transfusion.

It may be considered established that, in animals, after hæmorrhage, life may be restored by injecting the blood, defibrinated or not, provided it be introduced slowly, without admixture with air, and not in too great quantity. In the human subject, especially after hæmorrhage, the vital processes are sometimes restored by careful transfusion of human blood, with the above precautions; remembering that a very small quantity, three or four ounces, will sometimes be sufficient.

Quantity of Blood.—The determination of the entire quantity of blood contained in the body is a question of great interest, and has long engaged the attention of physiologists, without, however, any absolutely-definite results. Among those who have experimented on this point, may be mentioned Allen-Moulins, Herbst, Fried. Hoffmann, Valentin, Blake, Lehmann and Weber, and Vierordt. The fact that the labors of these eminent observers have so far been unsuccessful in determining definitely the entire quantity of blood shows the extent of the difficulties to be overcome before the question can be entirely settled. The chief difficulty lies in the fact that all the blood is not discharged from the body on division of the largest vessels, as after decapitation; and no perfectly-accurate means have been devised for estimating the quantity which remains in the vessels. The estimates of experimenters present the following wide differences: Allen-Moulins, who was one of the first to study this question, estimated the quantity of blood at one-twentieth the weight of the entire body. The estimate of Herbst was a little higher. Hoffmann estimated the quantity at one-fifth the weight of the body. These observers estimated the quantity remaining in the system after opening the vessels, by mere conjecture. Valentin was the first who attempted to overcome this difficulty by experiment. For this purpose he employed the following process: He took first a small quantity of blood from an animal for purposes of comparison; then he injected into the vessels a known quantity of a saline solution, and, taking another specimen of blood some time after, he ascertained by evaporation the proportion of water which it contained, and compared with the proportion in the first specimen. He reasoned that the excess of water in the second specimen over the first would give the proportion of the water introduced to the whole mass of blood; and, as the entire quantity of water introduced was known, the entire quantity of blood could be deduced therefrom. Suppose, for example, that the excess of water in the second specimen should be one part to ten of the blood, it would show that one part of water had been mixed with ten of the blood; and, if we had injected in all five ounces of water, we should have the whole quantity of blood ten times that, or fifty ounces. This method, however, is open to the objection that it is impossible to take note of the processes of imbibition and exhalation which are constantly in operation.

The following process, which is, perhaps, the one least open to sources of error, was employed by Lehmann and Weber, and applied directly to the human subject, in the case of two decapitated criminals: These observers estimated the blood remaining in the body after decapitation, by injecting the vessels with water until it came through nearly colorless. The liquid was carefully collected, evaporated to dryness, and the dry residue was assumed to represent a certain quantity of blood, the proportion of dry residue to a definite quantity of blood having been previously ascertained. If we could be certain that only the solid matter of the blood was thus removed, such an estimate would be tolerably accurate. As it is, we may consider it as approximating very nearly to the truth. We quote the following account of these observations:

"My friend, Ed. Weber, determined, with my coöperation, the weights of two criminals both before and after their decapitation. The quantity of blood which escaped from the body was determined in the following manner: Water was injected into the vessels of the trunk and head, until the fluid escaping from the veins had only a pale-red or yellow color; the quantity of the blood remaining in the body was then calculated, by instituting a comparison between the solid residue of this pale-red aqueous fluid, and that of the blood which first escaped. By way of illustration, I subjoin the results yielded by one of the experiments. The living body of one of the criminals weighed 60,140 grammes (132·7 pounds), and the same body after decapitation, 54,600 grammes; consequently, 5,540 grammes of blood had escaped. 28·560 grammes of this blood yielded 5·36 grammes of solid residue; 60·5 grammes of sanguineous water collected after the injection, contained 3·724 grammes of solid substances; 6,050 grammes of the sanguineous water that returned from the veins were collected, and these contained 37·24 grammes of solid residue, which corresponds to 1,980 grammes of blood; consequently, the body contained 7,520 grammes (16·59 pounds), 5,540 escaping in the act of decapitation, and 1,980 remaining in the body; hence, the weight of the whole blood was to that of the body nearly in the ratio of 1 : 8. The other experiment yielded a precisely similar result.

"It cannot be assumed that such experiments as these possess extreme accuracy, but they appear to have the advantage of giving in this manner the minimum of the blood contained in the body of an adult man; for although some solid substances, not belonging to the blood, may be taken up by the water from the parenchyma of the organs permeated with capillary vessels, the excess thus obtained is so completely counteracted by the deficiency caused by the retention of some blood in the capillaries, and in part by transudation, that our estimate of the quantity of blood contained in the human body may be considered as slightly below the actual quantity."

The process just described gives the most accurate idea of the probable quantity of blood in the human body; and, although more recent investigations have been made upon the lower animals, by different methods, they are all more or less open to objection. We may assume, then, that, in a person of ordinary muscular and adipose development, the proportion of blood to the weight of the body is about one to eight, the entire quantity of blood in the body being from sixteen to eighteen pounds. The relative quantity of blood is said to be less in the infant than in the adult, and to be diminished in old age. It has been found, also, in observations on the inferior animals, to be greater in the male than in the female.

Prolonged abstinence from food, except when large quantities of liquid are ingested, has a notable effect in diminishing the mass of blood, as indicated by the small quantity which can be removed from the body, under these circumstances, with impunity; and it has been experimentally demonstrated that the entire quantity of blood is considerably increased during digestion. Bernard drew from a rabbit weighing about two and a half pounds, during digestion, over ten and a half ounces of blood without producing death; while he found that the removal of half that quantity from an animal of the same size, fasting, was followed by death. Wrisberg has reported a case of a female criminal, very plethoric, from whom twenty-one pounds, seven and three-quarters ounces of blood flowed after decapitation. As the relations of the quantity of blood to the digestive function are so important, it is unfortunate that the conditions of the system in this respect were not noted in the observations of Lehmann and Weber. It is evident, therefore, that the quantity of blood in the body is considerably increased during digestion; but as regards the extent of this increase, we cannot form any very definite idea. It is only shown that there is a marked difference in the effects of hæmorrhage in animals, during digestion and fasting.

General Characters of the Blood.

Opacity.—The opacity of the blood depends upon the fact that it is not a homogeneous fluid, but is composed of two distinct elements, a clear plasma and corpuscles, which are both nearly transparent, but which have a different refractive power. If both of these elements had the same refractive power, the mixture would present no obstacle to the passage of light; but, as it is, the rays, which are refracted in passing from the air to the plasma, are again refracted when they enter the corpuscles, and again, when they pass from the corpuscles to the plasma, so that they are lost, even in a thin layer of the fluid. This loss of light in a mechanical mixture of two transparent liquids of unequal refractive power can be demonstrated by the following simple experiment: If to a little chloroform colored red, clear water be added in a test-tube, these liquids remain distinct from each other, and both are transparent; but if we agitate them violently, the chloroform is temporarily subdivided into globules and mixed with the water; and, as they refract light differently, the mixture is opaque.

Odor, Taste, Reaction, and Specific Gravity.—The blood has a faint but characteristic odor. This may be developed so as to be very distinct by the addition of a few drops of sulphuric acid, when an odor peculiar to the animal from which the blood has been taken becomes very marked.

The taste of the blood is faintly saline, on account of the presence of a considerable proportion, three or four parts per thousand, of chloride of sodium in the plasma.

The reaction of the blood is always distinctly alkaline. According to Zuntz, the alkalinity diminishes rapidly after the blood is drawn from the vessels. The alkaline reaction is due to the presence of basic carbonate and phosphate of soda in the plasma.

The specific gravity of defibrinated blood is from 1052 to 1057 (Robin), being somewhat less in the female than in the male. Its density varies greatly under different conditions of digestion.

Temperature.—The temperature of the blood is generally given as from 98° to 100° Fahr.; but recent experiments have shown that it varies considerably in different parts of the circulatory systsm, independently of exposure to the refrigerating influence of the atmosphere. By the use of very delicate registering thermometers, Bernard has succeeded in establishing the following facts with regard to the temperature in various parts of the circulatory system in dogs and sheep:

1. The blood is warmer in the right than in the left cavities of the heart.
2. It is warmer in the arteries than in the veins, with a few exceptions.
3. It is generally warmer in the portal vein than in the abdominal aorta, independently of the digestive act.
4. It is constantly warmer in the hepatic than in the portal veins.

He found the highest temperature in the blood of the hepatic vein, where it ranged from 101° to 107°. In the aorta, it ranged from 99° to 105°.

We may assume, then, in general terms, that the temperature of the blood in the deeper vessels is from 100° to 107° Fahrenheit.

Color of the Blood.—The color of the blood is due to the corpuscles. In the arterial system it is uniformly red. In the veins it is generally dark blue and sometimes almost black. This difference in color between the blood in the arterial and in the venous system was a matter of controversy at the time of Harvey. By the discoverer of the circulation, the difference, which is now universally known and admitted as regards most of the veins, was supposed to be merely accidental and dependent on external causes. Fifty years later, Lower demonstrated the change of color in the blood as it passes through the lungs, and associated it with the true cause; viz., the absorption of oxygen. The color in the veins, however, is not constant. Many years ago, John Hunter observed, in a case of syncope, that the blood drawn by venesection was bright red; and more recently, Bernard has demonstrated that, in some veins, the blood is nearly if not quite as red as in the arterial system. The color of the venous blood depends upon the condition of the organ or part from which it is returned. The red color was first noticed by Bernard in the renal veins, where it contrasts very strongly with the black blood in the vena cava. He afterward observed that the redness only existed during the functional activity of the kidneys; and when, from any cause, the secretion of urine was arrested, the blood became dark. He was led, from this observation, to examine the venous blood from other glands; and, directing his attention to those which he was able to examine during their functional activity, particularly the salivary glands, he found the blood red in the veins during secretion, but becoming dark as soon as secretion was arrested. These observations may be easily verified by opening the abdomen of a living animal, exposing the renal veins, and introducing a canula into the ureter, so as to be able to note the flow or arrest of the urine. So long as the urine continues to flow, the blood in these vessels is bright red; but when secretion becomes arrested, as it soon does after exposure of the organs, it presents no difference from the blood in the vena cava. In the submaxillary gland, by the galvanization of a certain nerve which he calls the motor nerve of the gland, Bernard has been able to produce secretion, and, by the galvanization of another nerve, to arrest it; in this way changing at will the color of the blood in the vein. It has been found by the same observer that division of the sympathetic in the neck, which dilates the vessels and increases the supply of blood to one side of the head, produces a red color of the blood in the jugular. He has also found that paralysis of a member by division of the nerve has the same effect on the blood returning by the veins.

The explanation of these facts is evident when we reflect upon the reasons why the blood is red in the arteries and dark in the veins. Its color depends upon the corpuscles; and as the blood passes through the lungs it loses carbonic acid and gains oxygen, changing from black to red. In its passage through the capillaries of the system, in the ordinary processes of nutrition, it loses oxygen and gains carbonic acid, changing from red to black. During the intervals of secretion, the glands receive just enough blood for their nutrition, and the ordinary interchange of gases takes place, with the consequent change of color; but, during their functional activity, the blood is supplied in greatly-increased quantity, in order to furnish the watery elements of the secretions. Under these circumstances, it does not lose oxygen and gain carbonic acid in any great quantity, as has been demonstrated by actual analysis, and consequently there is no marked change in color. When filaments of the sympathetic are divided, the vessels going to the part are dilated, and the supply of blood is increased to such an extent, that a certain proportion passes through without parting with its oxygen (a fact which has also been demonstrated by analysis), and consequently it retains its red color. The explanation in cases of syncope is probably the same, although this is merely a supposition. Even during secretion, a certain quantity of carbonic acid is formed in the gland, which, according to Bernard, is carried off in solution in the secreted fluid.

It may be stated, then, in general terms, that the color of the blood in the arteries is bright red; and, in the ordinary veins, like the cutaneous or muscular, it is dark blue, almost black. It is red in the veins coming from glands during secretion, and dark during the intervals of secretion.

Anatomical Elements of the Blood.

In 1661, the celebrated anatomist, Malpighi, in examining the blood of the hedgehog, with the imperfect lenses at his command, discovered little floating particles which he mistook for granules of fat, but which were the blood-corpuscles. He did not extend his observations in this direction; but, a few years later (1673), Leeuwenhoek, by the aid of simple lenses of his own construction, ranging in magnifying power from forty to one hundred and sixty diameters, first saw the corpuscles of human blood, which he minutely described in a paper published in the Philosophical Transactions, in 1674. To Leeuwenhoek is generally ascribed the honor of the discovery of the blood-corpuscles.[1] About a century later, William Hewson described another kind of corpuscles in the blood, which are much less abundant than the red, and which are now known under the name of white globules, or, as they have been called by Robin, leucocytes.

Without following the progress of microscopical investigations into the constitution of the blood, it may be stated that it is now known to be composed of a clear fluid, the plasma, or liquor sanguinis, holding certain corpuscles in suspension. These corpuscles are as follows:

1. Red corpuscles; by far the most abundant, constituting a little less than one-half of the mass of blood.
2. Leucocytes, or white corpuscles; much less abundant, existing only in the proportion of one to several hundred red corpuscles.
3. Granules; exceedingly minute, called, by Milne-Edwards, globulins, and, by Kölliker, elementary granules. These are few in number, and are probably fatty particles from the chyle. They are to be regarded as accidental constituents of the blood.

Red Corpuscles.—These little bodies give to the blood its red color and its opacity. They are true, organized structures, containing organic nitrogenized and inorganic elements molecularly united, and, as an exception to the general rule, a little fatty matter in union with the organic principles. They constitute a little less than one-half the mass

[1] Some writers give the credit of the discovery of the blood-corpuscles to Swammerdam. In 1658, Swammerdam studied the blood-corpuscles of the frog and described them very accurately; but his researches were not published until 1788, a number of years after his death. In questions of priority, it is usual to date discoveries from the time of their first publication.

of blood, and, according to the observations of all who have investigated this subject, are more abundant in the male than in the female.

The form of the blood-corpuscles is peculiar. They are flattened, biconcave, circular disks, with a thickness of from one-fourth to one-third of their diameter. Their edges are rounded, and the thin, central portion occupies about one-half of their diameter. Their consistence is not much greater than that of the plasma. They are very elastic, and, if deformed by pressure, immediately resume their original shape when the pressure is removed. Their specific gravity is from 1088 to 1105, considerably greater than the specific gravity of the plasma, which is about 1028. (Robin.)

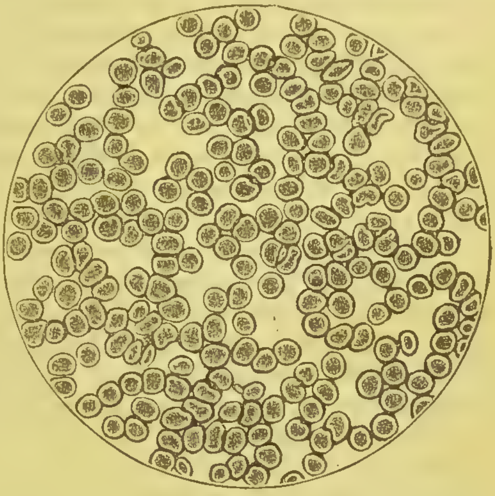


FIG. 1.—*Human blood-corpuscles; magnified* 370 *diameters.* (From a photograph taken at the United States Army Medical Museum.)

When the blood has been drawn from the vessels and coagulates slowly, the greater density of the red corpuscles causes them to gravitate to the lower portions of the clot, leaving the white corpuscles and fibrin at the surface. This is the cause of the "buffy-coat" mentioned by some writers. If coagulation be prevented by the addition of a small quantity of sulphate of soda, there is quite a marked gravitation of red corpuscles after standing for some hours.

The peculiar form of the blood-corpuscles gives them a very characteristic appearance under the microscope. Examined with a magnifying power of from three hundred to five hundred diameters, those which present their flat surfaces have a shaded centre when the edges are exactly in focus. This appearance was formerly supposed to indicate the existence of a nucleus having a constitution different from that of the rest of the corpuscle. It is now understood to be an optical effect, the result of the form of the corpuscles; their biconcavity rendering it impossible for the centre and edges to be exactly in focus at the same instant, so that, when the edges are in focus, the centre is dark, and, when the centre is bright, the edges are shaded.

As the blood-corpuscles are examined by the microscope by transmitted light, they are nearly transparent and of a pale-amber color. It is only when they are collected in masses that they present the red tint characteristic of blood as it appears to the naked eye. This yellow or amber tint is quite characteristic. A pretty good idea of the color may be obtained by largely diluting blood in a test-tube and holding it between the eye and the light.

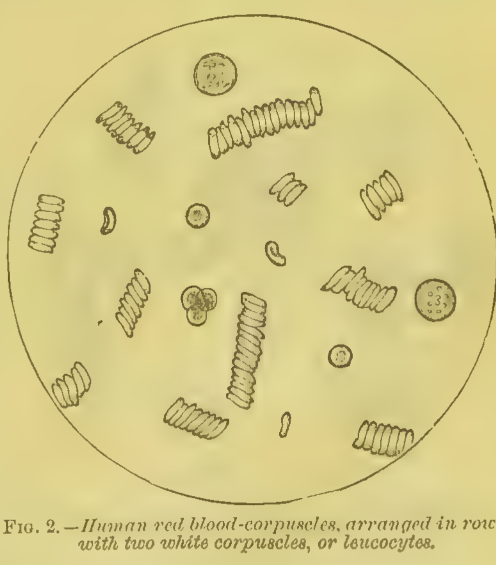


FIG. 2.—*Human red blood-corpuscles, arranged in rows, with two white corpuscles, or leucocytes.*

In examining blood under the microscope, the corpuscles are seen in many different positions; some flat, some on their edges, etc. This assists us in recognizing their peculiar form.

It has long been observed that the blood-corpuscles have a remarkable tendency to arrange themselves in rows like *rouleaux* of coin. This appearance has attracted universal attention, and for a long time it was not satisfactorily explained. Robin, however, has given what seems to be the true explanation. He has shown that, shortly after removal from the vessels, there exudes from the corpuscles an adhesive substance which smears their surface and causes them to stick together. Of course the tendency is to adhere by their flat surfaces. In examining a specimen of blood under the microscope, the presence of this adhesive exudation may be demonstrated by employing firm and gradual pressure on the glass cover, when the adherent corpuscles may be separated, in some instances, and, with oblique light, we can see a little transparent filament between them, which draws them together, as it were, when the pressure is removed. This phenomenon is due to a post-mortem change; but it occurs so soon, that it presents itself in nearly every specimen of fresh blood, and is therefore mentioned in connection with the normal characters of the blood-corpuscles.

Dimensions.—The diameter of the blood-corpuscles has a more than ordinary anatomical interest; for, varying perhaps less in size than other anatomical elements, they are often taken as the standard by which we form an idea of the size of other microscopic objects. The diameter usually given is $\frac{1}{3500}$ of an inch. The exact measurement given by Robin is .0073 of a millimetre, or $\frac{1}{3437}$ of an inch. It is stated by some authors that the size of the corpuscles is very variable, even in a single specimen of blood. We have repeatedly measured them and found a diameter of $\frac{1}{3500}$ of an inch. Very few are to be found which vary from this measurement. Kölliker, who gives their average diameter as $\frac{1}{3000}$ of an inch, states that "at least ninety-five out of every hundred corpuscles are of the same size."

We cannot leave the subject of the size of the blood-corpuscles without a notice of the measurements in the blood of different animals. This point is interesting, from the fact that it is often an important question to determine whether a given specimen of blood be from the human subject or from one of the inferior animals. Comparative measurements also have an interest on account of a relation which seems to exist in the animal scale between the size of the blood-corpuscles and muscular activity. In all the mammalia, with the exception of the camel and llama, in which the corpuscles are oval, the blood has nearly the same anatomical characters as in the human subject. In only two animals, the elephant and sloth, are the red corpuscles larger than in man; in all others, they are smaller, or of nearly the same diameter. By reference to the table, it will be seen that, in some animals, the corpuscles are very much smaller than in man; and, by accurate measurements, we are enabled to distinguish their blood from the blood of the human subject. But, in forming an opinion on this subject, it must be remembered that there is some variation in the size of the corpuscles of the same animal. We can easily distinguish the blood of the human subject, or of the mammals generally, from that of birds, fishes, or reptiles; for, in these classes of animals, the corpuscles are oval and contain a granular nucleus.

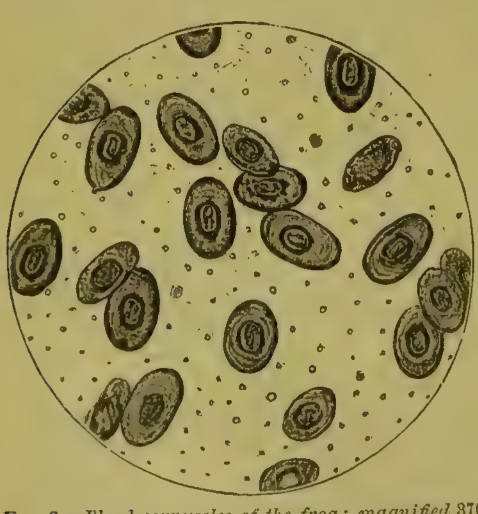


FIG. 3.—*Blood-corpuscles of the frog; magnified 870 diameters.* (From a photograph taken at the United States Army Medical Museum.)

Milne-Edwards has attempted to show, by a comparison of the diameter of the blood-corpuscles in different species, that their size bears an inverse ratio to the muscular activity of the animal. Reference to the table will show that this relation holds good to some extent, while there certainly exists none between the size of the corpuscles and the size of the animal. In deer, animals remarkable for muscular activity, the corpuscles are very small, $\frac{1}{5000}$ of an inch; while in the sloth they are $\frac{1}{2800}$, and in the ape, which is comparatively inactive, $\frac{1}{3400}$. But, on the other hand, in the dog, which is quite active, we have a corpuscle of $\frac{1}{3500}$ of an inch, and in the ox, which is certainly not so active, the diameter of the corpuscle is $\frac{1}{4200}$ of an inch. Although this relation between the size of the blood-corpuscles and muscular activity is not invariable, it is certain that, the higher we go in the great classes of animals, the smaller are the blood-corpuscles; the largest being found in the lowest orders of reptiles, and the smallest, in the mammalia. The blood of the invertebrates, with a few exceptions, contains no colored corpuscles.

Table of Measurements of Red Corpuscles.

This table is taken from the table of Mr. Gulliver, published in the Sydenham edition of Hewson's Works, page 237. Nearly five hundred measurements were made by Mr. Gulliver; and of these, one hundred of the most important have been selected. It will be observed that the diameter of the human blood-corpuscle is greater than that generally given. It must be borne in mind that all these measurements are mere approximations; but they are useful, as showing the relations of the corpuscles in different animals, and enabling us to distinguish the blood of the human subject from that of some of the inferior animals. The measurements are all given in fractions of an English inch; and, in making the selections, the common names of the animals have been substituted for the technical names given in the original.

Mammals.

Corpuscles Circular.

	Diameter.		Diameter.
Man,	$\frac{1}{3200}$	Weasel,	$\frac{1}{4205}$
Chimpanzee,	$\frac{1}{3412}$	Polecat,	$\frac{1}{4167}$
Ourang-outang,	$\frac{1}{3383}$	Otter,	$\frac{1}{3502}$
Black monkey,	$\frac{1}{3530}$	Seal,	$\frac{1}{3281}$
Red monkey,	$\frac{1}{3395}$	Porpoise,	$\frac{1}{3829}$
Cape baboon,	$\frac{1}{3568}$	Whale,	$\frac{1}{3099}$
Brown baboon,	$\frac{1}{3493}$	Hog,	$\frac{1}{4230}$
Dog-faced baboon,	$\frac{1}{3461}$	Indian elephant,	$\frac{1}{2745}$
Lazy monkey,	$\frac{1}{3691}$	Indian rhinoceros,	$\frac{1}{3765}$
Bat,	$\frac{1}{4175}$	Horse,	$\frac{1}{4600}$
Long-eared bat,	$\frac{1}{4465}$	Ass,	$\frac{1}{4000}$
Mole,	$\frac{1}{4747}$	Stag,	$\frac{1}{5088}$
Hedgehog,	$\frac{1}{4085}$	Fallow deer,	$\frac{1}{4515}$
Badger,	$\frac{1}{3940}$	Virginia deer,	$\frac{1}{5036}$
Polar bear,	$\frac{1}{3870}$	Giraffe,	$\frac{1}{4571}$
Brown bear of Europe,	$\frac{1}{3723}$	Antelope,	$\frac{1}{5108}$
Black bear of North America.	$\frac{1}{3693}$	Gazelle,	$\frac{1}{4922}$
Raccoon,	$\frac{1}{3950}$	Goat,	$\frac{1}{6366}$
Dog,	$\frac{1}{3542}$	Sheep,	$\frac{1}{5355}$
Fox,	$\frac{1}{4117}$	Ox,	$\frac{1}{4267}$
Jackal,	$\frac{1}{3860}$	Buffalo,	$\frac{1}{4586}$
Wolf,	$\frac{1}{3600}$	Musk deer of Java,	$\frac{1}{12325}$
Striped hyena,	$\frac{1}{3735}$	Flying squirrel,	$\frac{1}{3892}$
Spotted hyena,	$\frac{1}{3820}$	Red squirrel,	$\frac{1}{4000}$
Cat,	$\frac{1}{4404}$	Black squirrel,	$\frac{1}{3841}$
Lion,	$\frac{1}{4322}$	Gray squirrel,	$\frac{1}{4000}$
Tiger,	$\frac{1}{4206}$	Marmot,	$\frac{1}{3484}$
Leopard,	$\frac{1}{4319}$	Brown rat,	$\frac{1}{3911}$
Panther,	$\frac{1}{4616}$	Black rat,	$\frac{1}{3754}$
Ferret,	$\frac{1}{4134}$	Mouse,	$\frac{1}{3814}$

	Diameter.		Diameter.
Water rat,	$\frac{1}{3790}$	Opossum,	$\frac{1}{3567}$
Porcupine,	$\frac{1}{3369}$	Kangaroo,	$\frac{1}{3535}$
Beaver,	$\frac{1}{3325}$		
Guinea-pig,	$\frac{1}{3538}$		
Rabbit,	$\frac{1}{3607}$		
Two-toed sloth,	$\frac{1}{2865}$		

	L. diam.	S. diam.
Dromedary (oval),	$\frac{1}{3254}$	$\frac{1}{5921}$
Camel (oval),	$\frac{1}{3123}$	$\frac{1}{5876}$

Birds.

Corpuscles Oval.

	Long Diameter.	Short Diameter.		Long Diameter.	Short Diameter.
Eagle (ring-tailed),	$\frac{1}{1812}$	$\frac{1}{3832}$	Pigeon,	$\frac{1}{1973}$	$\frac{1}{3643}$
Owl,	$\frac{1}{1763}$	$\frac{1}{4076}$	Turtle-dove,	$\frac{1}{2005}$	$\frac{1}{3369}$
Jay,	$\frac{1}{2041}$	$\frac{1}{4167}$	Peacock,	$\frac{1}{1835}$	$\frac{1}{3589}$
Raven,	$\frac{1}{1961}$	$\frac{1}{4000}$	Cock,	$\frac{1}{2102}$	$\frac{1}{3466}$
Starling,	$\frac{1}{2115}$	$\frac{1}{3892}$	Turkey,	$\frac{1}{2045}$	$\frac{1}{3598}$
Wren,	$\frac{1}{2369}$	$\frac{1}{4133}$	Guinea-fowl,	$\frac{1}{2054}$	$\frac{1}{4415}$
Sparrow,	$\frac{1}{2140}$	$\frac{1}{3500}$	Quail,	$\frac{1}{2347}$	$\frac{1}{3470}$
Woodpecker,	$\frac{1}{2170}$	$\frac{1}{3892}$	Goose,	$\frac{1}{1866}$	$\frac{1}{3839}$
Swallow,	$\frac{1}{2133}$	$\frac{1}{4000}$	Swan,	$\frac{1}{1806}$	$\frac{1}{3692}$
Stork,	$\frac{1}{1755}$	$\frac{1}{3439}$	Duck,	$\frac{1}{1937}$	$\frac{1}{3424}$

Reptiles.

Corpuscles Oval.

	Long Diameter.	Short Diameter.		Long Diameter.	Short Diameter.
Green turtle,	$\frac{1}{1231}$	$\frac{1}{1882}$	Lizard,	$\frac{1}{1555}$	$\frac{1}{2743}$
Land tortoise,	$\frac{1}{1252}$	$\frac{1}{2216}$	Viper,	$\frac{1}{1274}$	$\frac{1}{1800}$

Amphibia.

Corpuscles Oval.

	Long Diameter.	Short Diameter.		Long Diameter.	Short Diameter.
Frog,	$\frac{1}{1108}$	$\frac{1}{1821}$	Toad,	$\frac{1}{1043}$	$\frac{1}{2000}$

Fishes.

Corpuscles Oval.

	Long Diameter.	Short Diameter.		Long Diameter.	Short Diameter.
Perch,	$\frac{1}{2099}$	$\frac{1}{2824}$	Pike,	$\frac{1}{2000}$	$\frac{1}{3555}$
Carp,	$\frac{1}{2141}$	$\frac{1}{3429}$	Eel,	$\frac{1}{1745}$	$\frac{1}{2842}$

Enumeration of the Blood-Corpuscles.—In most of the quantitative analyses of the blood, the proportion of moist corpuscles to the entire mass of blood is stated to be a little less than one-half. This estimate is necessarily rather rough; and it would be interesting to ascertain, if possible, the normal variations in the proportion of corpuscles, under different conditions of the system, particularly as these bodies play so important a part in many of the functions of the organism. Estimates of this kind have lately been made by Malassez, who has devised a method, more accurate than those employed before, for the actual enumeration of the red corpuscles, in which, it is stated, the error does not amount to more than two or three per cent. The process employed is the following:

The blood to be examined is diluted with ninety-nine parts of a liquid composed of one volume of a solution of gum-arabic of a specific gravity of 1020 with three volumes of a solution of equal parts of sulphate of soda and chloride of sodium, also of a specific gravity of 1020. The mixture, containing one part of blood in one hundred, is introduced into a small thermometer-tube with an elliptical bore, the sides of the tube being ground flat for convenience of microscopical examination. The capacity of the tube is to be calculated, by estimating the weight of a volume of mercury contained in a given length. The tube is then filled with the diluted blood, and the number of corpuscles in a given length of the tube is counted by means of a microscope fitted with an eye-piece micrometer. In this way, the number of corpuscles in a given volume of blood can be readily estimated. In man, the number in a cubic millimeter of blood (a millimeter = about $\frac{1}{25}$ of an inch) is estimated at about four million.

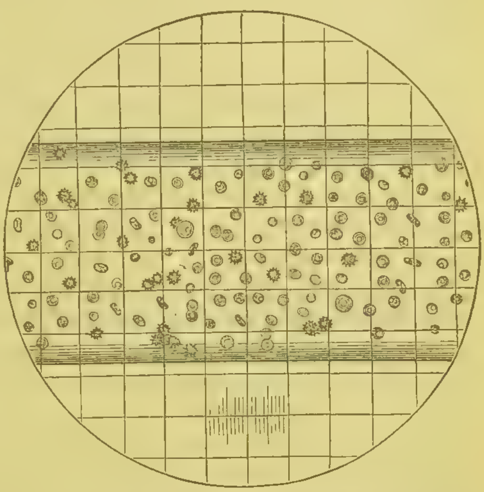


Fig. 4.—*Artificial capillary, filled with a sanguineous mixture, seen under a quadrilateral micrometer.* (Malassez.)

According to the observations of Malassez, the proportion of corpuscles is about the same in all parts of the arterial system. In the veins, the corpuscles are more abundant than in the arteries. In the venous system, the blood of the splenic veins presents the largest proportion of corpuscles, and the proportion is smallest in the blood of the hepatic veins. These results favor the idea that the red corpuscles are formed, to a certain extent, in the spleen, and that some are destroyed in the liver; but farther observations are necessary to render this view certain.

Post-mortem Changes in the Blood-Corpuscles.—In examining the fresh blood under the microscope, after the specimen has been under observation a short time, the corpuscles assume a peculiar appearance, from the development, on their surface, of very minute, rounded projections, like the granules of a raspberry. A little later, when they have become partly desiccated, they present a shrunken appearance, and their edges are more or less serrated. Under these conditions, their original form may be restored by adding to the specimen a liquid of about the density of the serum. When they have been completely dried, as in blood spilled upon clothing or on a floor, months or even years after, they can be made to assume their characteristic form by carefully moistening them with an appropriate liquid. This property is taken advantage of in examinations of old spots supposed to be blood; and, if the manipulations be carefully conducted, the corpuscles may be recognized without difficulty by the microscope.

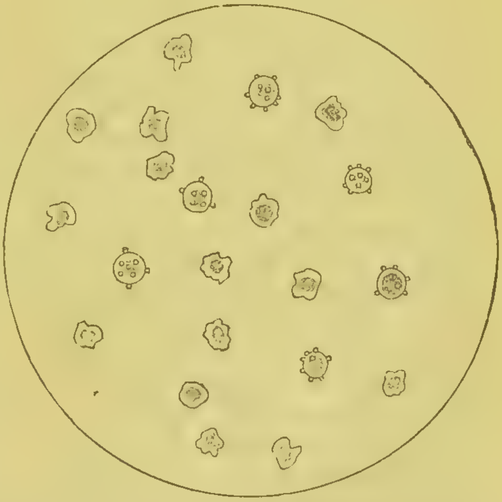


Fig. 5.—*Human blood-corpuscles, showing post-mortem alterations.*

If pure water be added to a specimen of blood under the microscope, the corpuscles swell up, become spherical, and are finally lost to view by solution. The same effect follows almost instantaneously on the addition of acetic acid.

Structure.—The structure of the blood-corpuscles is very simple. They are perfectly homogeneous, presenting, in their normal condition, no nuclei or granules, and are not provided with an investing membrane. A great deal has been said by anatomists concerning this latter point; and some are of the opinion that the corpuscles are cellular in their structure, being composed of a membrane, with viscid, semifluid contents. Without going fully into the discussion of this question, it may be stated that few have assumed to have actually demonstrated this membrane; but certain observers have inferred its existence from the fact of the corpuscles swelling, and, as they term it, bursting on the addition of water. The appearances presented upon the addition of iodine to blood previously treated with water, which have been supposed to indicate the presence of shreds of ruptured vesicles, are not sufficiently distinct to demonstrate the existence of a membrane. The great elasticity of the corpuscles, the persistence with which they preserve their biconcave form, and their general appearance, rather favor the idea that they are homogeneous bodies of a definite shape, than that they have a cell-wall with semifluid contents; especially as the existence of a membrane has been only inferred and not positively demonstrated. Their mode of nutrition is like that of other anatomical elements. They are bathed in a nutritive fluid, the plasma, and, as fast as their substance becomes worn out and effete, new material is supplied. In this way, they undergo the same molecular changes as other anatomical structures. When destroyed or removed from the body in hæmorrhages, new corpuscles are gradually developed, until their quantity reaches the normal standard.

Development of the Blood-Corpuscles.—Very early in the development of the ovum, the blood-vessels appear, constituting what is called the area vasculosa. At about the same time, the blood-corpuscles are developed, it may be before, or it may be just after the appearance of the vessels, for this point is undetermined. The blood becomes red when the embryon is about one-tenth of an inch in length. From this time until the end of the sixth or eighth week, they are from thirty to one hundred per cent. larger than in the adult. Most of them are circular, but some are ovoid, and a few are globular. At this period, nearly all of them are provided with a nucleus; but, from the first, there are some in which this is wanting. The nucleus is from $\frac{1}{7000}$ to $\frac{1}{5000}$ of an inch in diameter, globular, granular, and insoluble in water and acetic acid. As development advances, these nucleated corpuscles are gradually lost; but, even at the fourth month, we may still see a few remaining. After this time, they present no anatomical differences from the blood-corpuscles in the adult.

In many works on physiology and general anatomy, we find accounts of the development of the red corpuscles from the colorless corpuscles, or leucocytes, which are supposed to become disintegrated, their particles becoming developed into red corpuscles; but there seems to be no positive evidence that such a process takes place. The red corpuscles appear before the leucocytes are formed; and it is only the fact that the two varieties coexist in the blood-vessels which has given rise to such a theory. It is most reasonable to consider that the red corpuscles are formed by a true genesis in the sanguineous blastema. There is, farthermore, no sufficient evidence that any particular organ or organs have the function of producing the blood-corpuscles. It is regarded by some as a necessity that there should be an organ for the destruction of the corpuscles, and one for their formation. Regarding them, as we certainly must, as organized bodies which are essential anatomical elements of the blood, it is difficult to imagine what reasons, based on their function, should lead physiologists to seek so persistently after an organ for their destruction. The hypothesis that they are used in the formation of pigmentary matter seems hardly sufficient to account for this. The observations of Malassez, which show an increase in the number of corpuscles in the blood coming from the spleen and a diminution in the blood of the hepatic veins, are not sufficiently definite to serve as a demonstration that the spleen is a blood-forming organ; and the same remark may be applied to observations upon the formation of blood-corpuscles by the marrow of the bones.

In the present state of our knowledge, the following seem to be the most rational views with regard to the development and nutrition of the blood-corpuscles:

1. At the time of their first appearance in the ovum, they are formed by no special organs, for no special organs then exist; but they appear by genesis in the sanguineous blastema.

2. When fully formed, they are regularly-organized anatomical elements, subject to the same laws of gradual molecular waste and repair as any of the anatomical elements of the tissues.

3. They are generated *de novo* in the adult, when diminished in quantity by hæmorrhage or otherwise; and, under these circumstances, they are probably formed in the liquor sanguinis, by the same process by which they take their origin in the ovum.

Function of the Blood-Corpuscles.—Although the albuminoid constituents of the plasma of the blood are essential to nutrition, the red corpuscles are the parts most immediately necessary to life. We have already seen, in treating of transfusion, that life may be restored to an animal in which the functions have been suspended from hæmorrhage, by the introduction of fresh blood; and, while it is not necessary that this blood should contain the elements of fibrin, it has been shown by the experiments of Prévost and Dumas and others, that the introduction of serum, without the corpuscles, has no restorative effect. When all the arteries leading to a part are tied, the tissues lose their properties of contractility, sensibility, etc., which may be restored, however, by supplying it again with the vivifying fluid. We shall see, when we come to treat of the function of respiration, that one great distinction between the corpuscular and fluid elements of the blood is the great capacity which the former have for absorbing gases. Direct observations have shown that blood will absorb from ten to thirteen times as much oxygen as an equal bulk of water; and this is dependent almost entirely on the presence of the red corpuscles. As all the tissues are constantly absorbing oxygen and giving off carbonic acid, a very important function of the corpuscles is to carry oxygen to all parts of the body. In the present state of our knowledge, this is the only well-defined function which can be attributed to the red corpuscles, and it undoubtedly is the principal one. They have an affinity, though not so great, for carbonic acid, which, after the blood has circulated in the capillaries of the system, takes the place of the oxygen. In some experiments performed a few years ago on the effects of hæmorrhage and the seat of the "*besoin de respirer*," we demonstrated that one of the results of removal of blood from the system was a condition of asphyxia, dependent upon the absence of these respiratory elements.

Leucocytes, or White Corpuscles of the Blood.—In addition to the red corpuscles of the blood, this fluid always contains a number of colorless bodies, globular in form, in the substance of which are embedded a greater or less number of minute granules. These have been called by Robin, leucocytes. This name seems more appropriate than that of white or colorless blood-corpuscles, inasmuch as they are not peculiar to the blood, but are found in the lymph, chyle, pus, and various other fluids, in which they were formerly known by different names. All who have been in the habit of examining the animal fluids microscopically have noticed the great similarity between the corpuscular elements found in the above-mentioned situations; and, as microscopes have been improved and investigations have become more exact, the varieties of corpuscles have been narrowed down. It is now pretty generally acknowledged that the corpuscles found in mucus and pus are identical; also, that there is no difference between the white corpuscles found in the lymph, chyle, and blood; and, finally, it has been shown that all of these bodies, which were formerly supposed to present marked distinctive characters, belong to the same class, presenting but slight differences in different situations. The description which will be given of the white corpuscles of the blood, and the effects of reagents, will answer, in the main, for all the corpuscular bodies that are grouped under the name of leucocytes.

Leucocytes are normally found in the blood, lymph, chyle, semen, colostrum, and vitreous humor. Pathologically, they are found in the secretion of mucous membranes, following irritation, and in inflammatory products, when they are called pus-corpuscles.

In examining a specimen of blood with the microscope, we immediately notice the marked difference between the leucocytes and red corpuscles. The former are globular, with a smooth surface, somewhat opaque from the presence of more or less granular matter, white, and larger than the red corpuscles.

In examining the circulation under the microscope, we are struck with the adhesive character of the leucocytes as compared with the red corpuscles. The latter circulate with great rapidity in the centre of the vessels, while the leucocytes have a tendency to adhere to the sides, moving along slowly, and occasionally remaining for a time entirely stationary, until they are swept along by a change in the direction or force of the current.

The size of the leucocytes varies somewhat, even in any one fluid, such as the blood. Their average diameter may be stated as $\frac{1}{2500}$ of an inch. It is in pus, where they exist in greatest abundance, that their microscopical characters may be studied with greatest advantage. In this fluid, after it is discharged, the corpuscles sometimes present remarkable deformities. They become polygonal in shape, and sometimes ovoid, occasionally presenting projections from their surface, which give them a stellate appearance. These alterations, however, are only temporary; and, after from twelve to twenty-four hours, they resume their globular shape. On the addition of acetic acid, they swell up, become transparent, with a delicate outline, and present in their interior one, two, three, or even four rounded, nuclear bodies, generally collected in a mass. This is rather to be considered as a coagulation of a portion of the corpuscle, than a nucleus brought out by the action of the acid which renders the corpuscle transparent; although in some corpuscles it is seen without the addition of any reagent. This appearance is produced, though more slowly, by the addition of water.

Leucocytes vary considerably in their external characters in different situations. Sometimes they are very pale and almost without granulations, while at others they are filled with fatty granules and are not rendered clear by acetic acid. As a rule, they increase in size and become granular when confined in the tissues. In colostrum, where they are called colostrum-corpuscles, they generally undergo this change. As the result of inflammatory action, when they are sometimes called inflammatory or exudation-corpuscles, leucocytes frequently become much hypertrophied and are filled with fatty granules.

The deformation of the leucocytes, to which allusion has already been made, is sometimes so rapid and changeable as to produce creeping movements, due to the projection and retraction of portions of their substance. These movements are of the kind called amœboid, and are supposed to be important in the process of migration of the corpuscles, which has lately been described.

The quantity of leucocytes compared to the red corpuscles can only be given approximatively. It has been estimated by counting under the microscope the red corpuscles and leucocytes contained in a certain space. Moleschott gives the proportion as 1 : 335; others, at from 1 : 300 to 1 : 500. It has been found by Dr. E. Hirt, of Zittau, whose observations have been confirmed by others, that the relative quantity of leucocytes is much increased during digestion. He found, in one individual, a proportion of 1 : 1800 before breakfast; an hour after breakfast, which was taken at 8 o'clock, 1 : 700; between 11 and 1 o'clock, 1 : 1500; after dining, at 1 o'clock, 1 : 400; two hours after, 1 : 1475; after supper, at 8 P. M., 1 : 550; at 11½ P. M., 1 : 1200. The leucocytes are much lighter than the red corpuscles, and, when the blood coagulates slowly, are frequently found with a certain amount of colorless fibrin forming a layer on the surface of the clot, which is called the "buffy-coat." Their specific gravity is about 1070.

Numerous observers, among whom may be mentioned Donné, Kölliker, Gray, Hirt, and Malassez, have noticed a great increase in the number of leucocytes in the blood coming from the spleen, and have supposed that they are formed chiefly in this organ. It is inconsistent with the mode of development of these corpuscles to suppose that any special organ is exclusively engaged in their production; and their persistence in animals after extirpation of the spleen shows that they are developed in other situations.

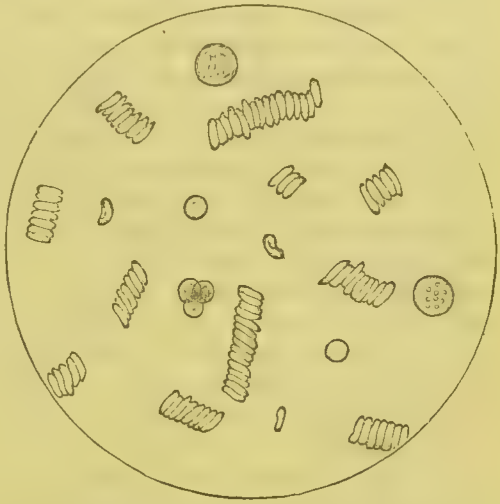


FIG. 6.—*Human red and white blood-corpuscles.*

The function of the leucocytes is not understood. The supposition that they break down and become nuclei for the development of red corpuscles, which at one time obtained, is a pure hypothesis, which has no positive basis in fact.

Development of Leucocytes.—These corpuscles appear in the blood-vessels very early in fœtal life, before the lymphatics can be demonstrated. They arise in the same way as the red corpuscles, by genesis from materials existing in the vessels. They appear in lymphatics, before these vessels pass through the lymphatic glands, in the fœtus anterior to the development of the spleen, and also on the surface of mucous membranes; so they cannot be considered as produced exclusively by the lymphatic glands, as has been supposed. There is no organ nor class of organs in the body specially charged with their formation; and, although they frequently appear as a result of inflammation, this process is by no means necessary for their production. Robin has carefully noted the phenomena of their development in recent wounds. The first exudation consists of clear fluid, with a few red corpuscles; then, a finely granular blastema. In from a quarter of an hour to an hour, pale, transparent globules, from $\frac{1}{8000}$ to $\frac{1}{6000}$ of an inch in diameter, make their appearance, which soon become finely granular and present the ordinary appearance of leucocytes. They are thus developed, like other anatomical elements, by organization of the necessary elements furnished by a blastema, and not by the action of any special organ or organs.

This view of the mode of development of leucocytes seems to be established by the following very elegant experiments of Onimus, showing that corpuscles may be developed, under favorable conditions, in a perfectly clear, homogeneous blastema:

Onimus used the clear fluid taken without delay from rapidly-developed blisters, which he found ordinarily contained no leucocytes, but which he carefully filtered in order to remove all sources of error. The filtered liquid contained no morphological elements; but, on the other hand, he found that, if the liquid were allowed to remain for an hour or more in contact with the derma, it always contained leucocytes and epithelial cells. Under these circumstances, even after filtration, the liquid contained a few leucocytes; but, after six or seven hours of repose in a conical vessel, the corpuscular elements gravitated to the bottom, leaving the upper portion of the liquid perfectly clear.

This liquid, entirely free from anatomical elements, was enclosed in little sacs formed of an animal membrane (gold-beater's skin) and introduced under the skin of a living rabbit. At the end of twelve hours, a few small leucocytes and granulations had made their appearance; at the end of twenty-four hours, the fluid had become somewhat opaque, and contained a large number of leucocytes and granulations; and, at the end of thirty-six hours, the fluid was white, milky, and composed almost entirely of leucocytes and granulations. The leucocytes, which were examined also by Prof. Robin, presented all the characters by which these corpuscles are ordinarily recognized. These experiments were repeated with more than forty different specimens of fluid from blisters.

The experiments were then varied in order to show the influence of the membrane and the composition of the blastema upon the development of leucocytes. By modifying the membrane in which the blastema was enclosed, it was found that the corpuscles were rapidly developed in proportion to the activity of the osmotic action. When thick animal membranes were used, their development was slow, and, in some instances, did not take place at all. There was no development of leucocytes in a clear blastema enclosed in a sac of caoutchouc or in glass tubes hermetically sealed; and from this it was concluded that osmotic action is a necessary condition, and that the mere heat of the body is not sufficient to develop these corpuscles, even in an appropriate blastema. The influence of this constant molecular movement is in striking contrast to the conditions of absolute repose which are so essential to the formation of crystals from ordinary saline solutions.

One of the most interesting points in these experiments is connected with the influence of the composition of the blastema upon the development of leucocytes. It was found that these bodies were never developed in a blastema in which the fibrin had been coagulated. Experimenting with two liquids, the only difference in their constitution being that in one the fibrin had been coagulated by repeatedly plunging the glass tube in which it was contained into cool water, while the other was kept at the ordinary temperature, a little bicarbonate of soda being added to prevent coagulation, it was found that leucocytes were developed as usual in the fluid which contained the fibrinous elements, and that none appeared in the other. On placing the liquid with its coagulum enclosed in a sac under the skin, it was found that, after a time, the fibrin was redissolved, but no leucocytes made their appearance.

The theory which has for its motto, *omnis cellula e cellula*, receives no support from these experiments. Onimus added to fluids which had been deprived of fibrinous matters, epithelial cells and pus-corpuscles, but, even after thirty-six hours, he never found any additional development of corpuscular elements. Leucocytes added to fluids in which the fibrinous elements were unchanged did not seem to exert any influence upon the development of new corpuscles.

Elementary Corpuscles.—Little granules are found in the blood, especially during digestion, which, as they were supposed to take part in the formation of the white corpuscles, have been called elementary granules or corpuscles. They probably are little fatty particles of the chyle which come from the thoracic duct, and are not positively known to have any connection with the formation of the other corpuscular elements of the blood.

Composition of the Red Corpuscles.

The red corpuscles of the blood contain an organic nitrogenized principle, called globuline, combined with inorganic principles and a coloring matter. The composition of the leucocytes has not been accurately determined. The inorganic matters contained in the red corpuscles are in a condition of intimate union with the other constituents, and can only be separated by incineration. It may be stated, in general terms, that most, if not all of the various inorganic constituents of the plasma exist also in the corpuscles, which latter are particularly rich in the salts of potassa. Iron exists in the coloring matter of the corpuscles. In addition, the corpuscles contain cholesterine, lecethine, a certain amount of fatty matter, and probably some of the organic saline principles of the blood.

Globuline.—Rollett, by alternately freezing and thawing blood several times in succession in a platinum vessel, has succeeded in separating the coloring matter from the red corpuscles. When the blood is afterward warmed and liquefied, the fluid is no longer opaque, but is dark and transparent. Microscopical examination then reveals the corpuscles, entirely decolorized and floating in a red, semitransparent serum. Denis extracted the organic principle of the corpuscles by adding to defibrinated blood about one-half its volume of a solution of chloride of sodium containing one part in ten of water. Allowing this to stand for from ten to fifteen hours, there appears a viscid mass, which is very carefully washed with water until all the coloring matter and the salt added has been removed. The whitish, translucid mass which remains is called globuline. Denis has also extracted a small quantity of fibrin from the corpuscles. Globuline is readily extracted from the blood of birds, but is obtained with difficulty from the blood of the human subject.

Hæmaglobine.—This is the coloring matter of the red corpuscles. It has been called by different writers, hæmaglobuline or hæmatocrystalline; but the crystals called hæmatine and hæmatosine are derivatives of hæmaglobine and are not true proximate principles. Hæmaglobine may be extracted from the red corpuscles by adding to them, when congealed, ether, drop by drop. A jelly-like mass is then formed, which is passed rapidly through a cloth, crystals soon appearing in the liquid, which may be separated by filtration. (Gautier.)

The crystals of hæmaglobine extracted from human blood are in the form of four-sided prisms, elongated rhomboids, or rectangular tablets, of a purplish-red color. They are composed of carbon, hydrogen, oxygen, nitrogen, sulphur, and a small quantity of iron. They are soluble in water and in very dilute alkaline solutions, and the hæmaglobine is precipitated from these solutions by ferrocyanide of potassium, nitrate of mercury, chlorine, or acetic acid. The proportion of this coloring matter to the entire mass of blood is about one hundred and twenty-seven parts per thousand. It constitutes from $\frac{12}{13}$ to $\frac{9}{10}$ of the dried corpuscles. A solution of hæmaglobine in one thousand parts, examined with the spectroscope, gives two dark bands between the letters D and E in Frauenhofer's scale.

Treated with oxygen or prepared in fluids in contact with the air, there occurs a union of oxygen with the coloring matter, forming what has been called oxyhæmaglobine. There can be no doubt that the oxygen enters into an intimate, though rather unstable combination with hæmaglobine, and this is an important point to be considered in connection with the absorption of oxygen by the blood in respiration. A solution of oxyhæmaglobine presents a different spectrum from a solution of pure hæmaglobine. If we examine a solution of oxyhæmaglobine with the spectroscope and then discharge the oxygen by prolonged ebullition in a vacuum, the characteristic bands of pure hæmaglobine make their appearance. The union of oxygen with hæmaglobine is unstable and the oxgen can be removed by a current of hydrogen, nitrous oxide, or carbonic acid. A current of carbonic oxide displaces the oxygen, and the carbonic oxide forms a very stable combination with the coloring matter. It is well known that carbonic oxide is a very poisonous gas, which becomes fixed in the corpuscles so that they become incapable of absorbing oxygen.

According to recent observations, oxygen combined with hæmaglobine exists in the condition of ozone. A solution of oxyhæmaglobine is readily decomposed by a current of sulphuretted hydrogen, forming, like ozone, water and a precipitate of sulphur.

2

Hæmatine may be produced by decomposition of hæmaglobine, by a process which it is not necessary to describe, as the hæmatine is not a proximate principle. Hæmatoidine is also a product of decomposition of hæmaglobine, but it does not contain iron. Hæmatoidine is more interesting, however, from the fact that it is frequently found in old clots that have been long extravasated in the tissues. Robin found a notable quantity of crystals of hæmatoidine in a cyst of the liver.

FIG. 7.—*Crystallized hæmaglobine.* (Gautier.) *a*, *b*, crystals from the venous blood of man; *c*, blood of the cat; *d*, blood of the Guinea pig; *e*, blood of the marmot; *f*, blood of the squirrel. (Gautier.)

Assuming, as we certainly may, that the blood furnishes material for the nourishment of all the tissues and organs, we should expect to find entering into its composition all the proximate principles existing in the body which undergo no change in nutrition, like the inorganic principles, and organic matters capable of being converted into the organic elements of every tissue. Farthermore, as the products of waste are all taken up by the blood before their final elimination, these also should enter into its composition. With these facts in our minds, we can readily appreciate the importance of accurate proximate analyses of the circulating fluid.

Notwithstanding the immense amount of labor bestowed by the most eminent chemists of the day upon the quantitative analysis of the blood, and the great physiological interest attaching to every advance in our knowledge in this direction, the chemical difficulties involved are so great, that even now there are no analyses which give the exact quantities of each of its inorganic constituents. This is owing to the great difficulty in the analysis of any fluid in which inorganic and organic principles are so closely united; for there is no more delicate problem in analytical chemistry than the determination of the presence and the proportions of inorganic substances united with organic matter. Of the animal fluids which are easily obtained, the blood, from the large proportion of different organic principles which enter into its composition, presents the greatest difficulties to the analytical chemist. Another difficulty is the necessity of a proximate, and not an ultimate analysis. It is not sufficient to give the amount of certain chemical elements which the blood contains; we must ascertain the amount of these elements in the state of union with each other to form proximate principles.

Most of the constituents of the blood are found both in the corpuscles and plasma. It is difficult to determine all of the different constituents of these two parts of the blood. It has been shown, however, by Schmidt, of Dorpat, that the phosphorized fats are more abundant in the globules, while the fatty acids are more abundant in the plasma. The salts with a potash-base have been found by the same observer to exist almost entirely in the corpuscles, and the soda-salts are four times more abundant in the plasma than in the corpuscles. In addition to the nutritive principles, we have, entering into the composition of the blood, urea, cholesterine, urate of soda, creatine, creatinine, and other substances the characters of which are not yet fully determined, belonging to the class of excrementitious principles. Their consideration comes more appropriately under the head of excretion, and they will be fully taken up in the chapters devoted to that subject.

Analysis of the Blood.

In the analyses given in the older works on physiology, the blood, having been divided into plasma and corpuscles, was supposed to contain, in the plasma, two organic principles, called albumen and fibrin. Recent investigations, however, have shown that the organic constituents of the plasma are more complex; and the more modern analyses of the blood give other organic principles, which have been separated by new methods. As these have been very generally accepted by modern writers, it becomes necessary to describe them in detail, and we shall adopt the new nomenclature, as far as the different organic principles have been established by definite observations. An argument in favor of this subdivision of the matters formerly recognized as fibrin and albumen is the fact, which has long been apparent, that the organic constituents of the blood, particularly albumen, are known to possess certain peculiar properties which distinguish them from these principles as they are found elsewhere. The following table, which we have carefully compiled from recent authorities, particularly Robin, gives approximatively the quantities of the different constituents of the blood-plasma. These may be divided into the following classes: 1. Inorganic principles; 2. Organic saline principles; 3. Organic non-nitrogenized principles; 4. Excrementitious matters; 5. Organic nitrogenized principles.

Composition of the Blood-Plasma.

Specific gravity, 1,028.

Inorganic principles.	Water, 779 parts per 1,000 in the male; 791 parts per 1,000 in the female.	
	Chloride of sodium, 3 to 4 parts per 1,000.	
	" " potassium, 0·359 parts per 1,000.	
	" " ammonium, proportion not determined.	
	Sulphate of potassa, 0·288 parts per 1,000.	
	" " soda, proportion not determined.	
	Carbonate of potassa, " " "	
	" " soda (with bicarbonate of soda), 1·200 parts per 1,000.	
	" " lime, proportion not determined.	
	" " magnesia, " " "	
	Phosphate of lime of the bones, and neutral phosphate,	1·500 parts per 1,000.
	" " magnesia,	
	" " potassa,	
	" " iron (probable),	
	Basic phosphates and neutral phosphate of soda,	
	Silica, copper, lead, and magnesia, traces occasionally.	
Organic saline principles.	Lactate of soda, proportion not determined.	
	" " lime (probable), proportion not determined.	
	Pneumate of soda, " " "	
	Oleate of soda,	1·475 parts per 1,000.
	Margarate of soda,	
	Stearate " "	
	Valerate " "	
	Butyrate " "	
Organic non-nitrogenized principles.	Oleine,	
	Margarine,	
	Stearine,	
	Lecethine, containing nitrogen and called phosphorized fatty matter, 0·400 parts per 1,000.	
	Glucose, 0·002 parts per 1,000.	
	Glycogenic matter, proportion not determined.	
	Inosite (muscles), " " "	

Excrementitious matters.	Carbonic acid in solution.
	Urea, 0·177 parts per 1,000, in arterial blood; 0·088, in the blood of the renal vein.
	Urate of soda, proportion not determined.
	" " potassa (probable), proportion not determined.
	" " lime, " " " "
	" " magnesia, " " " "
	" " ammonia, " " " "
	Sudorates of soda, etc., " " "
	Inosates, " " "
	Oxalates, " " "
	Creatinine, " " "
	Leucine, " " "
	Hypoxanthine, " " "
	Cholesterine, 0·455 to 0·751 parts per 1,000, in the entire blood.
Organic nitrogenized principles.	Plasmine, 25 parts (dried) per 1,000. { Fibrin, 3 parts per 1,000. Metalbumen, 22 parts per 1,000.
	Serine, 53 parts (dried) per 1,000.
	(Moist fibrin, 8·820 parts per 1,000, in the entire blood. Metalbumen and serine constitute the albumen of the older analyses. Albumen, about 75 parts [dried] and 330 parts [moist] per 1,000, in the entire blood.)
	Peptones, 4 parts (dried) and 28 parts (moist) per 1,000.
	Coloring matters of the plasma, proportion and characters not determined.

We shall take the above table as a guide for our study of the individual constituents of the blood-plasma. As regards gases, in addition to carbonic acid, which we have classed with the excrementitious matters, the blood contains oxygen, nitrogen, and hydrogen. The nitrogen and hydrogen are not important, and the relations of oxygen will be fully considered under the head of respiration. Most of the coloring matter of the blood exists in the red corpuscles, which contain a peculiar principle which we have already considered in connection with the chemical constitution of these bodies.

In studying the composition of the blood, as well as the composition of food, the tissues, secreted fluids, etc., it is convenient to divide its constituents into classes, and this we have done in the simplest manner possible.

It is evident, the blood receiving all the products of disassimilation as well as the nutritive principles resulting from digestion, that there should be a division of its constituents into nutritive and excrementitious. We have classed certain principles together as excrementitious. These are the various products of disassimilation of the organism, which are taken up by the blood or conveyed to the blood-vessels by the lymphatics, exist in the blood in small quantity, and are constantly being separated from the blood by the different excreting organs. Their constant removal from the blood is the explanation of the excessively minute proportion in which they exist in this fluid. Their relations to the organism will be fully considered under the head of excretion.

Excluding, then, for the present, all consideration of the products of disassimilation, we have to study the various constituents of the blood that are more or less directly concerned in nutrition.

Physiological chemists recognize certain constituents of the organism, called proximate principles, which may be elementary substances, but which are more frequently compounds. We speak of chloride of sodium as a proximate principle existing in the blood, because, as chloride of sodium, it gives to the blood certain properties. We do not regard the chemical elements, chlorine and sodium, as proximate principles, because they do not exist in the blood uncombined. Still, a proximate principle may be a chemical element, as in the case of oxygen, which, as oxygen, performs, in the blood, certain important functions.

Adopting, in the main, the definition given by Robin, we may regard as a proximate principle, a substance extracted from the body, which cannot be subdivided without chemical decomposition and loss of certain characteristic properties. This definition will apply to all classes of proximate principles, organic as well as inorganic.

Taking as a basis, the classification proposed by Robin, we may divide the proximate principles of the blood, and, indeed, of the entire organism, as follows:

1. *Inorganic Principles.*—This class is of inorganic origin, definite chemical composition, and crystallizable. The substances forming it are all introduced from without, and are all discharged from the body in the same form in which they entered. They never exist alone, but are always combined with the organic principles, to form the organized fluids or solids. This union is "atom to atom," and so intimate that they are taken up with the organic elements, as the latter are worn out and become effete, and are discharged from the body, although themselves unchanged. To supply the place of the principles thus thrown off, a fresh quantity is deposited in the process of nutrition. They give to the various organs important properties; and, although identical with substances in the inorganic world, in the interior of the body, they behave as organic substances. They require no special preparation for absorption, but are soluble and taken in unchanged. They are received into the body in about the same proportion at all periods of life, but their discharge is notably diminished in old age, giving rise to calcareous incrustations and deposits and a considerable increase in the calcareous matter entering into the composition of the tissues. As examples of this class we may cite water, chloride of sodium, the carbonates, sulphates, phosphates, and other inorganic salts.

The functions of water in the blood are sufficiently evident. It acts as a solvent for the inorganic salts, the organic salts, and the excrementitious matters. In conjunction with the nitrogenized principles, it constitutes a medium in which the corpuscles are suspended without solution.

The various salts enumerated in the table exist in solution in water and are more or less intimately combined with the coagulable organic principles. Of these, the chloride of sodium is the most abundant. It undoubtedly has an important function in giving density to the plasma and in regulating the processes of endosmosis and exosmosis. In connection with the organic salts and crystallizable excrementitious matters, it may be stated, in general terms, that the blood contains from 14 to 16 parts per 1,000 of matters in actual solution, of which from 6 to 8 parts consist of inorganic salts. The presence of these principles in solution, with the organic coagulable principles, prevents the solution of the corpuscular elements of the blood. The presence of the chlorides and the alkaline sulphates assists in dissolving the sulphates, carbonates, and the calcareous phosphates. A portion of the carbonates and phosphates are decomposed in the system and furnish bases for certain of the organic salts, such as the lactates, urates, etc.

2. *Organic Saline Principles.*—These principles are for the most part formed in the organism, and they exist in the blood in very small quantity. The lactates are probably produced by decomposition of a portion of the bicarbonates and the union of the bases with lactic acid, the lactic acid resulting from a change of a portion of the saccharine matter in the blood. The pneumate of soda is the result of the union of pneumic acid, an acid principle found in the lungs, with the base. The physiological relations of these principles are little understood. The salts formed by the union of fatty acids with bases are probably produced by decomposition of the fatty principles, a great part of which is derived from the food.

3. *Organic Non-nitrogenized Principles.*—These usually exist in the blood in small quantity and are derived mainly from the food. Lecethine, although it contains nitrogen, is introduced into this class because it presents many of the properties of the fats. It exists in the blood, bile, nervous substance, and the yolk of egg. This principle is supposed by Robin to be almost identical with protagon. Its chemical properties and physiological relations are not well understood. The saccharine principles and glyco-

genic matter are derived in part from the food and in part from the liver, where sugar and glycogenic matter are manufactured. They are of organic origin, definite chemical composition, and crystallizable. The fats and sugars are distinguished from other organic principles by the fact that they are composed of carbon, hydrogen, and oxygen. In the sugars, the hydrogen and oxygen exist in the proportion to form water, which fact has given them the name of hydrocarbons or hydrates of carbon. The principles of this class play an important part in development and nutrition. One of them, sugar, appears very early in fœtal life, formed first by the placenta, and afterward by the liver, its formation by the latter organ continuing during life. Fat is a necessary element of food, and is also formed in the interior of the body. The exact influence which these substances have on development and nutrition is not known; but experiments and observation have shown that this influence is important. They will be considered more fully under the head of nutrition.

4. *Excrementitious Matters.*—A full consideration of these principles, which are all formed by the process of disassimilation of the tissues and are taken up by the blood to be eliminated by the proper organs, belongs to excretion. The relations of carbonic acid to the system will be fully considered in connection with respiration.

5. *Organic Nitrogenized Principles.*—This class of proximate principles is of organic origin, indefinite chemical composition, and non-crystallizable. Substances forming this class are apparently the only principles which are endowed with so-called vital properties, taking materials for their regeneration from the nutritive fluids and appropriating them to form part of their own substance. Considered from this point of view, they are different from any thing which is met with out of the living body. They are all, in the body, in a state of continual change, wearing out and becoming effete, when they are transformed into excrementitious substances. The process of repair in this instance is not the same as in inorganic substances, which enter and are discharged from the body without undergoing any change. The analogous substances which exist in food undergo a very elaborate preparation by digestion, before they can even be absorbed by the blood-vessels; and still another change takes place when they are appropriated by the various tissues. They exist in all the solids, semisolids, and fluids of the body, never alone, but always combined with inorganic substances. As a peculiarity of chemical constitution, they all contain nitrogen, which has given them the name of nitrogenized or azotized principles. In studying their properties more fully, we shall see that they are by far the most important elements in the organism. The elaborate preparation which they require for absorption involves the most important part of the function of digestion. Their absolute integrity is necessary to the operation of the essential functions of many tissues, as muscular contraction or conduction of nervous force. An exact knowledge of all the transformations which take place in their regeneration and the process by which they are converted into effete or excrementitious matters would enable us to comprehend nutrition, which is the most important part of physiology; but as yet we know little of these changes, and may consider ourselves fortunate in understanding a few of the laws in accordance with which they are regulated.

Of the different classes of proximate principles existing in the blood, it is at once apparent that the organic nitrogenized principles are more complex in their constitution, properties, and functions than the other classes. These principles, as they exist in the blood, possess peculiar and characteristic properties, which it will be necessary to study in detail.

Plasmine, Fibrin, Metalbumen, Serine.—The name plasmine was given by Denis to a peculiar principle which he extracted from the blood by the following process: The blood drawn directly from an artery or vein is received into a vessel containing one-seventh part of its volume of a concentrated solution of sulphate of soda, which prevents coagulation; in a short time the corpuscles gravitate to the bottom of the vessel, and the plasma may be separated by decantation; to the plasma is added an excess of pulverized chloride of sodium, when a soft, pulpy substance is precipitated, which is plasmine. This substance, after desiccation, bears a proportion of about twenty-five parts per thousand of blood. It is soluble in from ten to twenty parts of water, when a portion of it coagulates and may be removed by stirring with twigs or a bundle of broom-corn, in the way in which fibrin is separated from the blood. The fibrin thus separated is called by Denis concrete fibrin, and the substance which remains in solution, dissolved fibrin. By most writers of the present day, the dissolved fibrin of Denis is called metalbumen, a name which we shall adopt.

According to Denis, plasmine is a proximate principle of the blood, and, after extraction by the process just described, is decomposed into concrete fibrin and dissolved fibrin, or metalbumen. Having removed the concrete fibrin from the solution of plasmine, the metalbumen is coagulated by the addition of sulphate of magnesia, which does not coagulate ordinary albumen. The proportion of dried metalbumen in the blood is about twenty-two parts per thousand. The proportion of dried fibrin is about three parts per thousand.

After the extraction of plasmine from the blood, another coagulable substance remains, which is called serine. This is coagulated by heat, the strong mineral acids, and absolute alcohol, but is not coagulated by ether, which coagulates albumen of the white of egg. Serine bears a close resemblance to ordinary albumen, but is stated to be much more osmotic. Its proportion, desiccated, in the blood is about fifty-three parts per thousand.

We cannot admit the existence of new coagulable principles in the blood unless it be shown that the processes by which they are extracted do not involve decomposition of established proximate constituents. The processes just described do not seem to involve artificial decomposition. It is perfectly proper, in analyzing the blood, to prevent spontaneous coagulation by the addition of the sulphate of soda, as this salt simply keeps the blood fluid without apparently changing its organic constituents, and the plasmine is simply precipitated by the chloride of sodium. It is evident, also, that the substance called metalbumen, being coagulated by sulphate of magnesia, is not albumen, and serine also presents some important points of difference from albumen. Admitting the existence, then, of plasmine and serine, it is important to understand clearly the characters of these principles as compared with what were formerly called fibrin and albumen.

Instead of fibrin and albumen in the blood, we now recognize two new principles, in the natural condition of the circulating fluid, which are called plasmine and serine. The substance known as fibrin is one of the products of decomposition of plasmine. Metalbumen and serine constitute what was formerly called albumen. Fibrin is not a proximate principle, but is formed in the spontaneous decomposition of plasmine. Metalbumen is the other product of decomposition of plasmine. The fibrin of arterial blood has long been known to differ somewhat from the fibrin of venous blood, when the blood has been allowed to coagulate spontaneously. Arterial fibrin is insoluble in a solution of chloride of sodium which will dissolve the fibrin of venous blood.

Peptones, etc.—A certain quantity of nitrogenized matter, distinct from the principles just described, has been extracted from the blood, which is analogous to peptone or albuminose. This is separated by coagulating the serum of the blood with hot acetic acid and filtering, when the peptones pass through in the filtrate. These principles are probably derived from the food. Their proportion in the plasma is about four parts, dried, per thousand, or twenty-eight parts before desiccation.

A small quantity of coloring matter exists in the plasma. If we separate the corpuscles as completely as possible, the clear liquid still has a reddish-amber color. This coloring matter has never been isolated and studied. It is analogous to the coloring matters of the red corpuscles, the bile, and the urine.

In addition to the organic nitrogenized principles which we have described, some authors recognize a substance called paraglobuline, or fibrinoplastic matter, and fibrinogenic matter. These are supposed to be factors of fibrin, which come together in the coagulation of the blood. They will be considered in connection with the theories of coagulation. The so-called albuminates of soda and potassa have not been positively established as proximate principles.

Coagulation of the Blood.

The remarkable property in the blood of spontaneous coagulation has been recognized almost as far back as we can look into the history of physiology; and, since the discovery of the circulation, there have been few subjects connected with the physiology of the blood which have excited more universal interest; but the ideas with regard to the cause of this phenomenon were for a long time entirely speculative. The first definite experiments upon this subject were performed by Malpighi. He was followed by Borelli, Ruysch, and a host of others, who hold conspicuous places in the history of our science, among whom may be mentioned Hunter, Hewson, Müller, Thackrah, J. Davy, Magendie, Nasse, and Dumas. Although much labor has been expended on this subject, the final cause of coagulation is by no means definitely settled.

The blood retains its fluidity while it remains in the vessels and circulation is not interfered with. It is then composed, as we have seen, of a clear plasma, holding corpuscles in suspension. Shortly after the circulation is interrupted, or after blood is drawn from the vessels, it coagulates or "sets" into a jelly-like mass. In a few hours, we find that contraction has taken place, and a clear, straw-colored fluid has been expressed, the blood thus separating into a solid portion, the crassamentum, or clot, and a liquid, which is called serum. The serum contains all the elements of the blood except the red corpuscles and fibrin, which together form the clot. Coagulation takes place in the blood of all animals, commencing a variable time after its removal from the vessels. In the human subject, according to Nasse, when the blood is received into a moderately-deep, smooth vessel, the phenomena of coagulation present themselves in the following order:

First, a gelatinous pellicle forms on the surface, which occurs in from one minute and forty-five seconds to six minutes; in from two to seven minutes, a gelatinous layer has formed on the sides of the vessel; and the whole mass becomes of a jelly-like consistence, in from seven to sixteen minutes. Contraction then begins, and, if we watch the surface of the clot, we see little drops of clear serum making their appearance. This fluid increases in quantity, and, in from ten to twelve hours, separation is complete. The clot, which is heavier, sinks to the bottom of the vessel, unless it contain bubbles of gas or the surface be very concave. In most of the warm-blooded animals, the blood coagulates more rapidly than in man. It is particularly rapid in the class of birds, in some of which it takes place almost instantaneously. Observations have shown that coagulation is more rapid in arterial than in venous blood. In the former, the proportion of fibrin formed is notably greater, and, as we have seen, the characters of the fibrin are somewhat different. A solution of chloride of sodium dissolves the fibrin of venous blood, but does not dissolve the fibrin of an arterial clot.

The relative proportions of the serum and clot are very variable, unless we include in our estimate of the serum that portion which is retained between the meshes of the coagulated mass. As the clot is composed of corpuscles and fibrin, and as these in their moist state represent in general terms about one-half of the blood, it may be stated that, after coagulation, the actual proportions of the clot and serum are about equal. If we take simply the serum which separates spontaneously, we have a large quantity when the clot is densely contracted, and a very small quantity when it is loose and soft. Usually, the clot retains about one-fifth of the serum.

Characters of the Clot.—On removing the clot, after the separation of the serum is complete, it presents a gelatinous consistence, and is more or less firm, according to the degree of contraction which has taken place. As a general rule, when coagulation has been rapid, the clot is soft and but slightly contracted. When, on the other hand, coagulation has been slow, it contracts for a long time and is much denser. When coagulation is slow, the clot frequently presents what is known as the cupped appearance, having a concave surface, a phenomenon which depends merely on the extent of its contraction. It also presents a marked difference in color at its upper portion. The blood having remained fluid for some time, the red corpuscles settle, by virtue of their greater weight, leaving a colorless layer on the top. This is the buffy-coat spoken of by some authors. Although this frequently presents itself in the blood drawn in inflammations, it is by no means pathognomonic of this condition, and is liable to occur whenever coagulation is slow or has been retarded by artificial means. It is always present in the blood of the horse. Examined microscopically, the buffy-coat presents fibrils of coagulated fibrin with some of the white corpuscles of the blood. On removing a clot of venous blood from the serum, the upper surface is florid from contact with the air, while the rest of it is dark; and, on making a section, if the coagulation have not been too rapid, the gravitation of the red corpuscles is apparent. The section, which is at first almost black, soon becomes red from contact with the atmosphere. If the clot be cut into small pieces, it will undergo farther contraction, and express a part of the contained serum. If the clot be washed under a stream of water, at the same time kneading it with the fingers, we may remove almost all the red corpuscles, leaving the meshes of fibrin, which, on microscopical examination, presents the fibrillated appearance to which we have already referred.

Characters of the Serum.—After coagulation, if the serum be carefully removed, it is found to be a fluid of a color varying from a light amber to quite a deep, but clear red. This depends upon a peculiar coloring matter which has never been isolated. The specific gravity of the serum is about 1028, somewhat less than that of the entire mass of blood. It contains all the principles found in the plasma, or liquor sanguinis, with the exception of the elements of fibrin. It can hardly be called a physiological fluid, as it is formed only after coagulation of the blood and never exists isolated in the body. The effusions which are commonly called serum, although they resemble this fluid in some particulars, are not identical with it, being formed by a process of transudation rather than separation from the blood, as in coagulation. The serum must not be confounded with the plasma or liquor sanguinis, which is the natural clear portion of the blood.

Coagulating Principle of the Blood.—Acquainted, as we are, with the properties of fibrin, it is evident that this substance is the agent which produces coagulation of the blood. In fact, whatever coagulates spontaneously is called fibrin, and whatever requires some agent to produce this change of consistence is called by another name. But, before the properties of fibrin were fully understood, the question of the coagulating principle was a matter of much discussion. Malpighi was probably the first to isolate fibrin, which he did by washing the clot in a stream of water, which removed the corpuscles and left a whitish, fibrous net-work. His experiments are set forth in an article in which he attempted to show that the so-called polypi of the heart were formed of fibrin, although it was not then called by that name. These observations were soon confirmed by others; and it then became a question whether this substance existed as a fluid in the liquor sanguinis, or was furnished by the corpuscles after the removal of blood from the vessels. This was decided by Hewson, whose simple and conclusive experiments leave no doubt that coagulation of the blood is due to fibrin, and that this substance is entirely distinct from, and independent of the corpuscles. This observer, taking advantage of the property possessed by certain saline substances of preventing the coagulation of the blood, was the first to separate the liquor sanguinis from the corpuscles. He mixed fresh blood with a little sulphate of soda, which prevented coagulation, and, after the mixture had been allowed to stand for a time, the corpuscles gravitated to the bottom of the vessel. The clear fluid was then decanted and diluted with twice its quantity of water, when fibrin became coagulated.

The facts thus demonstrated by Hewson were confirmed by Müller, in 1832. He succeeded in separating the plasma from the corpuscles in the blood of the frog by simple filtration, first diluting it with a saccharine solution. The great size of the corpuscles in this animal prevents their passage through a filter, and the clear fluid which is thus separated soon forms a colorless coagulum.

From these observations, it is evident that the coagulation of the blood is due to the formation of fibrin. Coagulation of this substance first causes the whole mass of blood to assume a gelatinous consistence; and, by virtue of its contractile properties, it soon expresses the serum, while the red corpuscles are retained. One of the causes which operate to retain the corpuscles in the clot is the adhesive matter which covers their surface after they escape from the vessels, which produces the arrangement in rows like piles of coin, which we have already noted under the head of microscopical appearances. This undoubtedly prevents those which are near the surface from escaping from the clot during its contraction.

Circumstances which modify Coagulation out of the Body.—The conditions which modify coagulation of the blood have been closely studied by Hewson, Davy, Thackrah, Robin and Verdeil, and others. They are, in brief, the following:

Blood flowing slowly from a small orifice is more rapidly coagulated than when it is discharged in a full stream from a large orifice. If it be received into a shallow vessel, it coagulates much more rapidly than when received into a deep vessel. If the vessel be rough, coagulation is more rapid than if it be smooth and polished. If the blood, as it flows, be received on a cloth or a bundle of twigs, it coagulates almost instantaneously. In short, it appears that all circumstances which favor exposure of the blood to the air hasten its coagulation. The blood will coagulate more rapidly in a vacuum than in the air.

Coagulation of the blood is prevented by rapid freezing, but it takes place afterward when the fluid is carefully thawed. Between 32° and 140° Fahr., elevation of temperature increases the rapidity of coagulation. According to Richardson, agitation of the blood in closed vessels retards, and in open vessels hastens coagulation.

Various chemical substances retard or prevent coagulation. Among them we may mention the following: solutions of potash and of soda; carbonate of soda; carbonate of ammonia; carbonate of potash; ammonia; sulphate of soda. In the menstrual flow, the blood is kept fluid by mixture with the abundant secretions of the vaginal mucous membrane.

Coagulation of the Blood in the Organism.—The blood coagulates in the vessels after death, though less rapidly than when removed from the body. As a general proposition, it may be stated that this takes place in from twelve to twenty-four hours after circulation has ceased. Under these circumstances, the blood is found chiefly in the venous system, as the arteries are generally emptied by post-mortem contraction of their muscular coat; but, in the veins, coagulation is slow and imperfect. Coagula are found, however, in the left side of the heart and in the aorta, but they are much smaller than those in the right side of the heart and in the large veins. These coagula present the general characters we have already described. They are frequently covered by a soft, whitish film, analogous to the buffy-coat, and are dark in their interior.

It was supposed by John Hunter that coagulation of the blood did not take place in animals killed by lightning, or by prolonged muscular exertion, as when hunted to death; but it appears from the observations of others that this view is not correct. J. Davy reported a case of death by lightning where a loose coagulum was found in the heart twenty-four hours after. In this case, decomposition was very far advanced, and it is probable that the coagulum had become less firm from that cause. His observations also show that coagulation occurs after poisoning by hydrocyanic acid, and in animals hunted to death.

Coagulation in different parts of the vascular system is by no means unusual during life. In the heart, we sometimes find coagula which bear evidence of having existed for some time before death. These were called polypi by some of the older writers, and are often formed of fibrin almost free from red corpuscles. They generally occur when death is very gradual and when the circulation continues for some time with greatly-diminished activity. It is probable that a small coagulum is first formed, from which the corpuscles are washed away by the current of blood; that this becomes larger by farther depositions, until we have large, vermicular masses of fibrin, attached, in some instances, to the chordæ tendineæ. Clots produced in this way may be distinguished from those formed after death by their whitish color, dense consistence, and the closeness with which they adhere to the walls of the heart.

Bodies projecting into the caliber of a blood-vessel soon become coated with a layer of fibrin. Rough concretions about the orifices of the heart frequently induce the deposition of little masses of fibrin, which sometimes become detached and are carried to various parts of the circulatory system, as the lungs or brain, plugging up one or more of the smaller vessels. The experiment has been made of passing a thread through a small artery, allowing it to remain for a few hours, when it is found coated with a layer of coagulated fibrin.

Blood generally coagulates when effused into the areolar tissue or into any of the cavities of the body; although, effused into the serous cavities, the tunica vaginalis for example, it has been known to remain fluid for days and even weeks, and coagulate when let out by an incision. In the Graafian follicles, after the discharge of the ovum, we sometimes have the cavity filled with blood, which forms a clot and is slowly removed by absorption.

Coagulation thus takes place in the vessels as the result of stasis or of very great retardation of the circulation, and in the tissues or cavities of the body, whenever it is accidentally effused. In the latter case, it is generally removed in the course of time by absorption. This takes place in the following way: First, we have disappearance of the red corpuscles, or decoloration of the clot, and the fibrin is then the only substance which remains. This becomes reduced from a fibrillated to a granular condition, softens, finally becomes amorphous, and is absorbed; although, when the size of the clot is considerable, this may occupy weeks, and even months, and may never be completely effected. Effused in this manner, the constituents of the blood act as foreign bodies; the corpuscles cease to be organized anatomical elements capable of self-regeneration, break down, and are absorbed. The fibrin which remains undergoes the same process, the stages through which it passes being always those of decay, and not of development. In other words, the clot is incapable of organization.

Office of the Coagulation of the Blood in arresting Hæmorrhage.—The property of the blood under consideration has a most important office in the arrest of hæmorrhage. The effect of an absence or great diminution of the coagulability of the circulating fluid is exemplified in instances of what is called the hæmorrhagic diathesis; a condition in which slight wounds are apt to be followed by alarming, and it may be fatal hæmorrhage. This condition of the blood is not characterized by any peculiar symptoms except the obstinate flow of blood from slight wounds; and this may continue for years. In a case which came under our observation a few years since, excision of the tonsils was followed by bleeding, which continued for several days, and was arrested with great difficulty. On inquiry it was ascertained that the patient, a young man about twenty years of age, in other respects perfectly healthy, had been subject from early life to persistent hæmorrhage from slight wounds.

Circumstances which accelerate coagulation have a tendency to arrest hæmorrhage. It is well known that exposure of a bleeding surface to the air has this effect. The way in which the vessel is divided has an important influence. A clean cut will bleed more freely than a ragged laceration. In division of large vessels, this difference is sometimes very marked. Cases are on record in which the arm has been torn off at the shoulder-joint, and yet the hæmorrhage was, for a time, spontaneously arrested; while we know that division of an artery of comparatively small size, if it be cut across, would be fatal if left to itself. Under these circumstances, the internal coat is torn in shreds, which retract, their curled ends projecting into the caliber of the vessel and having the same effect on the coagulation of blood as a bundle of twigs. In laceration of such a large vessel as the axillary artery, the arrest cannot be permanent, for, as soon as the system recovers from the shock, the contractions of the heart will force out the coagulated blood which has closed the opening.

From the foregoing considerations, it is evident that the remarkable phenomenon of coagulation of the blood, which has so much engaged the attention of physiologists, has rather a mechanical than a vital function; for its chief office is in the arrest of hæmorrhage. Coagulation never takes place in the organism, unless the blood be in an abnormal condition with respect to circulation. Here its operations are mainly conservative; but, as almost all conservative processes are sometimes perverted, clots in the body may be productive of injury, as in the instances of cerebral apoplexy, clots in the heart occurring before death, the detachment of emboli, etc.

Cause of the Coagulation of the Blood.—If we adopt the views regarding the composition of the blood which involve the production of fibrin as a result of the decomposition of plasmine, we must change *in toto* our ideas of the cause of the coagulation of the blood. According to our present ideas, fibrin does not exist as a proximate principle, and plasmine is never decomposed in the body, under perfectly normal conditions; but, if the blood be drawn from the body, effused from the vessels, or if the circulation be arrested for a certain time, plasmine is decomposed, fibrin is formed, and the blood coagulates.

In another work, written in 1864, we discussed the question of the cause of the coagulation of the blood quite fully; but fibrin was then generally regarded as a proximate principle itself, and not as a product of decomposition. The theory that we then adopted was the one proposed by Richardson, in 1856; viz., that the blood normally contains a small quantity of ammonia, the presence of which keeps the fibrin in a liquid state; that ammonia is constantly being taken up by the blood from the tissues and exhaled by the lungs, and that, when the circulation of the blood is arrested, or when the blood is effused or drawn from the vessels, ammonia is exhaled and coagulation takes place. This theory has been formally abandoned by Richardson, who adheres, however, to the accuracy of his experiments. If these experiments be entirely reliable, they seem to prove the theory; but it is stated by Robin, that, using chemical processes which will detect $\frac{1}{1,000,000}$ of ammonia, not a trace of this substance is to be found in the blood; that a small quantity of ammonia added to the blood does not prevent coagulation; and that the blood secured against evaporation will nevertheless coagulate. The chemical experiments of Richardson were not very delicate, and the objections to them, made by Robin, are probably well-founded. We are justified, therefore, in abandoning the theory that coagulation of the blood is due to the evolution of ammonia.

We may take the same position with regard to the older theories of coagulation, which were nearly all vague and unsatisfactory. The idea that exposure to the air is the cause of coagulation, which was held by Hewson, is disproved by the simple fact that coagulation takes place in a vacuum. The vital theory of Hunter, which was adopted by most physiologists of his time, is too indefinite for discussion at the present day, and really expresses utter want of knowledge on the subject. The theory that motion is the cause of the fluidity of fibrin in the body, is disproved by the fact that violent agitation of the blood out of the body does not prevent coagulation; and thus it is with nearly all the theories that have been advanced.

The idea which we have to present does not explain why the blood coagulates, but it gives a certain notion of the probable conditions under which plasmine exists in the circulating fluid:

Plasmine, circulating in the blood-vessels, under normal conditions, is a liquid, and its decomposition into metalbumen and fibrin is abnormal. Plasmine is undoubtedly an important nutritive principle, and is constantly undergoing change as it is used in the nutrition of the nitrogenized constituents of the various tissues and organs, the material thus expended being supplied by the nitrogenized constituents of the food. It is, therefore, like other nitrogenized constituents of the organism, in a condition of constant metamorphosis; and all that we can say is that, while in this condition, getting material from some parts and giving off matters in others, it does not undergo those decomposing changes which are observed when it is effused, drawn from the body, or the circulation is arrested, which involve coagulation of the blood.

The above expresses nearly all that we positively know of the cause of the coagulation of the blood; but the question in fact reduces itself to the rather unsatisfactory proposition that the blood coagulates because, when its nitrogenized principles are removed from those constant molecular changes which are characteristic of the class of nitrogenized principles as they exist in the living organism, decomposition takes place, which results in the production of a coagulating matter. It is hardly to be expected that physiologists would be satisfied with this, which is indeed little more than a confession of ignorance; but it must be remembered that we are very little acquainted with the molecular changes taking place constantly in the living body. When we understand these more thoroughly, we may obtain a better knowledge of the causes of coagulation of the blood, cadaveric rigidity of muscles, and other changes which take place when the processes of nutrition cease.

Within the last few years, A. Schmidt (1861) has proposed a theory of coagulation which involves the coming together of certain principles called fibrin-factors. This theory has been adopted and more or less modified by Kühne, Virchow, and others. If blood-plasma, rendered neutral with acetic acid, be diluted with ten times its volume of water at 32° Fahr. and then be treated with a current of carbonic-acid gas, a flocculent precipitate is formed, which has been called paraglobuline, or fibrinoplastic matter. This substance may be dissolved in water containing air or oxygen in solution. After this precipitate has been separated, if the clear liquid be diluted with about twice its volume of ice-cold water and be again treated for a long time with a current of carbonic acid, a viscid scum is produced, which has been called fibrinogen. A small quantity of fibrinogen added to a solution of paraglobuline produces coagulation of a substance like fibrin. More recently, a third principle, a ferment, has been described by Schmidt, which he considers necessary to the formation of fibrin.

It is very questionable whether the substances called paraglobuline and fibrinogen exist in the blood as peculiar principles. Robin considers paraglobuline as identical with metalbumen, which is itself one of the products of the decomposition of plasmine. It is true that the so-called fibrinogen added to the liquid of hydrocele or other serosities not spontaneously coagulable produces coagulation, but this occurs, though more slowly, when the serum separated from the coagulated blood is added to these liquids.

It is more in accordance with our positive knowledge to state that we understand nothing with regard to the cause of coagulation of the blood beyond the fact that plasmine, when removed from its normal condition in the circulation, decomposes into coagulating fibrin and metalbumen, than to admit the existence of fibrinogen, a ferment, and paraglobuline, all of which may be products of decomposition.

It is a curious fact that leech-drawn blood remains fluid in the body of the animal. Richardson has observed, also, that the blood flowing from a leech-bite presents the same persistent fluidity, which explains the well-known fact that the insignificant wound gives rise to considerable hæmorrhage. On this point he has made the following curious experiment:

"After the leech was removed from the arm, the wound it had produced continued to give out blood very freely. I caught the blood thus flowing at different intervals, allowing it to trickle into teaspoons of the same size and shape. The results were curious. The blood which was received into the first spoon, and which was collected immediately after the removal of the leech, was dark, and showed the same feebleness of coagulation as the blood taken from the leech itself. Another portion of blood, received into a second spoon five minutes later, coagulated in twenty-five minutes with moderate firmness. A third portion of blood, caught ten minutes later still, coagulated in eight minutes; while at the end of half an hour the blood which still flowed from the wound coagulated firmly, and in fine red clots, in two minutes. Ultimately the blood coagulated as it slowly oozed from the wound, so that the wound itself was sealed up."

The existence of projections into the caliber of vessels, or the passage of a fine thread through an artery or vein, will determine the formation of a small coagulum upon the foreign substance, while the circulation is neither interrupted nor retarded. These facts demand explanation; but all we can say with regard to them is, that, in the present state of our knowledge, explanation is difficult, if not impossible. The process, under these circumstances, cannot be subjected to direct experiment, as in the case of blood coagulating out of the body; but a reasonable inference is that the foreign substance arrests the circulation of a certain portion of plasmine, which then undergoes decomposition.

During coagulation, fibrin assumes a filamentous form, presenting, under the microscope, the appearance of rectilinear fibrillæ. These fibrillæ gradually increase in number and, as contraction of the clot occurs, becomes irregularly crossed. They are always

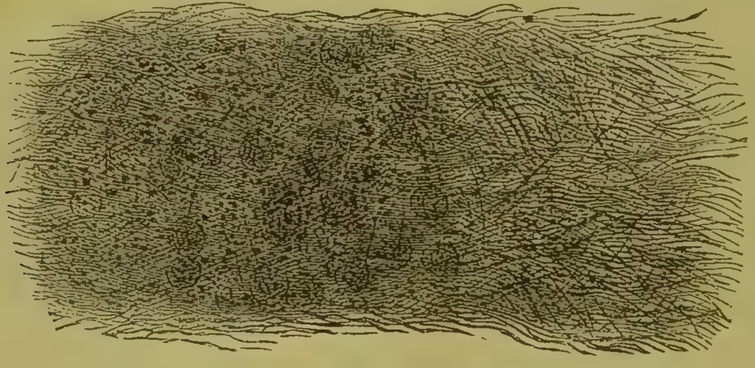


Fig. 8.—*Coagulated fibrin.* (Robin.)
Fibrinous clot, without red corpuscles, and containing leucocytes, thrown off in the form of a whitish pseudo-membrane in a case of ulceration of the neck of the uterus with hæmorrhage.

straight, however, and never assume the undulating appearance characteristic of the white fibrous tissue. The appearance just described does not indicate a process of organization. When fibrin is effused into any of the tissues or organs from rupture of vessels, it acts as a foreign substance, and, in time, becomes entirely or in part absorbed. The gradual production of membranes of new formation, as one of the results of inflammation, these becoming organized, is entirely different from sudden hæmorrhagic effusions.

The blood of the renal and hepatic veins, capillary blood, and the blood which passes from the capillary system into the veins after death, does not generally coagulate or coagulates very imperfectly; in other words, these varieties of blood do not readily form fibrin. The reason of this peculiarity is not known; but the fact affords a partial explanation of the normal fluidity of the blood; for this fluid, passing over the entire course of the circulation in about thirty seconds, seems to be constantly losing its coagulability in its passage through the liver, kidneys, and the general capillary system, as fast as its coagulability is increased in the other parts. Taking into consideration the rapidity of the circulation, it is evident that the blood cannot coagulate while the normal circulation is maintained, and while it is undergoing the constant changes incident to general nutrition.

CHAPTER II.

CIRCULATION OF THE BLOOD—ACTION OF THE HEART.

Discovery of the circulation—Physiological anatomy of the heart—Valves of the heart—Movements of the heart—Impulse of the heart—Succession of movements of the heart—Force of the heart's action—Action of the valves—Sounds of the heart—Causes of the sounds of the heart—Frequency of the heart's action—Influence of age—Influence of digestion—Influence of posture and muscular exertion—Influence of exercise—Influence of temperature—Influence of respiration on the action of the heart—Cause of the rhythmical contractions of the heart—Influence of the nervous system on the heart—Division of the pneumogastrics—Galvanization of the pneumogastrics—Causes of arrest of action of the heart—Blows upon the epigastrium.

Harvey discovered the circulation of the blood in 1616, taught it in his public lectures in 1619, and, in 1628, published the "*Exercitatio Anatomica de Motu Cordis et Sanguinis in Animalibus.*" This momentous discovery, from the isolated facts bearing upon it which were observed by anatomists, to its grand culmination with Harvey, so fully illustrates the gradual development of most great physiological truths, that it does not seem out of place to begin our study of the circulation with a rapid sketch of its history.

The facts bearing upon the circulation, which were developed before the time of Harvey, were chiefly anatomical. The writings of Hippocrates are very indefinite upon all points connected with the circulatory system; and no clear and positive statements are to be found in ancient works before the time of Aristotle. The work of Aristotle most frequently quoted by physiologists is his "History of Animals;" and in this occurs a passage which seems to indicate that he thought that air passed from the lungs to the heart; but in his work, *De Partibus Animalium*, it is stated that there are two great blood-vessels, the vena cava and aorta, arising from the heart, and that the aorta and its branches carry blood. Galen, however, demonstrated experimentally the presence of blood in the arteries, by including a portion of one of these vessels between two ligatures, in a living animal; but his ideas of the communication between the arteries and veins were erroneous, for he believed in the existence of small orifices in the septum between the ventricles of the heart, a mistake that was corrected by Vesalius, at about the middle of the sixteenth century.

In 1553, Michael Servetus, who is generally regarded as the discoverer of the passage of the blood through the lungs, or the pulmonary circulation, described in a work on theology the course of the blood through the lungs, from the right to the left side of the heart. This description, complete as it is, was merely incidental to the development of a theory with regard to the formation of the soul, and the development of what were called animal and vital spirits (*spiritus*). The same year, at the instigation of Calvin, Servetus was burned alive at Geneva, and a copy of his book was also committed to the flames. But one or two copies of this work are now in existence. One is in the library of the Institute of France, and bears evidence, in some pages that are partially burned, of the fate which it so narrowly escaped.

A few years later, Columbo, professor of anatomy at Padua, and Cesalpinus, of Pisa, described the passage of the blood through the lungs, though probably without any knowledge of what had been written by Servetus. To Cesalpinus is attributed the first use of the expression circulation of the blood. He also remarked that, after ligature or compression of veins, the swelling is always below the point of obstruction.

The history of the discovery of the valves in the veins is quite obscure, although priority of observation is almost universally conceded to Fabricius. As regards this point, we can depend only upon the dates of published memoirs, notwithstanding the assertion of Fabricius, that he had seen the valves in 1574. In 1545, Étienne described, in branches of the portal vein, "valves, which he called apophyses, and which he compared to the valves of the heart." In 1551, Amatus Lusitanus published a letter from Cannanus, in which it is stated that he had found valves in certain of the veins. In 1563, Eustachius published an account of the valves of the coronary vein. In 1586, a clear account, by Piccolhominus, of the valves of the veins was published. Fabricius gave the most accurate descriptions and delineations of the valves, and his first publication is said to have appeared in 1603. He demonstrated them to Harvey, at Padua; and it is probable that this was the origin of the first speculations by Harvey on the mechanism of the circulation. Shortly after the return of Harvey from Padua in 1602, he advanced beyond the study of inanimate parts by dissections, and investigated animated nature by means of vivisections. As is evident, when we consider the state of science at that time, anatomists had long been preparing the way for the discovery of the circulation, although they knew little of the functions of the parts they described. The conformation of the heart and vessels, and even the arrangement of the valves of the veins, did not lead them to suspect the course of the blood; but a few well-conceived experiments on living animals have made it appear so simple, that we now wonder it remained unknown so long. Furthermore, these experiments made it evident that there was a communication at the periphery between the arteries and the veins.

In the work of Harvey are described, first the movements of the heart, which he exposed and studied in living animals. He described minutely all the phenomena which accompany its action; its diastole, when it is filled with blood, and its systole, when the fibres of which the ventricles are composed contract simultaneously, and "by an admirable adjustment all the internal surfaces are drawn together, as if with cords, and so is the charge of blood expelled with force." From the description of the action of the ventricles, he passes to the auricles, and shows how these, by their contraction, fill the ventricles with blood. By experiments upon serpents and fishes, he proved that the blood fills the heart from the veins, and is sent out into the arteries. Exposing the heart and great vessels in these animals, he applied a ligature to the veins, which had the effect of cutting off the supply from the heart so that it became pale and flaccid; and by removing the ligature the blood could be seen flowing into the organ. When, on the contrary, a ligature was applied to the artery, the heart became unusually distended, which continued so long as the obstruction remained. When the ligature was removed, the heart soon returned to its normal condition.

The descriptions given by Harvey were the result of numerous experiments upon living animals; exposing the heart of cold-blooded animals, in which the movements are comparatively slow; studying, also, the action of this organ in warm-blooded animals, after its movements had become enfeebled. As we shall see when we come to describe the movements of the heart, nothing can exceed the simplicity and accuracy of the descriptions of Harvey, which are universally acknowledged to be correct in almost every particular.

Harvey completed his description of the circulation, by experiments showing the course of the blood in the arteries and veins and the uses of the valves of the veins.

These experiments are models of simplicity and pertinence. First, he showed that a ligature tightly applied to a limb prevented the blood from entering the artery and arrested pulsation. The ligature then relaxed and applied with moderate tightness so as to compress only the superficial veins allowed the blood to pass into the part by the arteries, but prevented its return by the veins, which consequently became excessively congested. The ligature being removed, the veins soon emptied themselves and the member regained its ordinary appearance. He observed the "knots" in the veins of the arm when a ligature was applied, as for phlebotomy, and showed that the space between these knots, which are formed by the valves, could be emptied of blood by pressing toward the heart, and would not fill itself while the finger was kept at the lower extremity. It was impossible, by pressure with the fingers, to force the blood back through one of the valves.

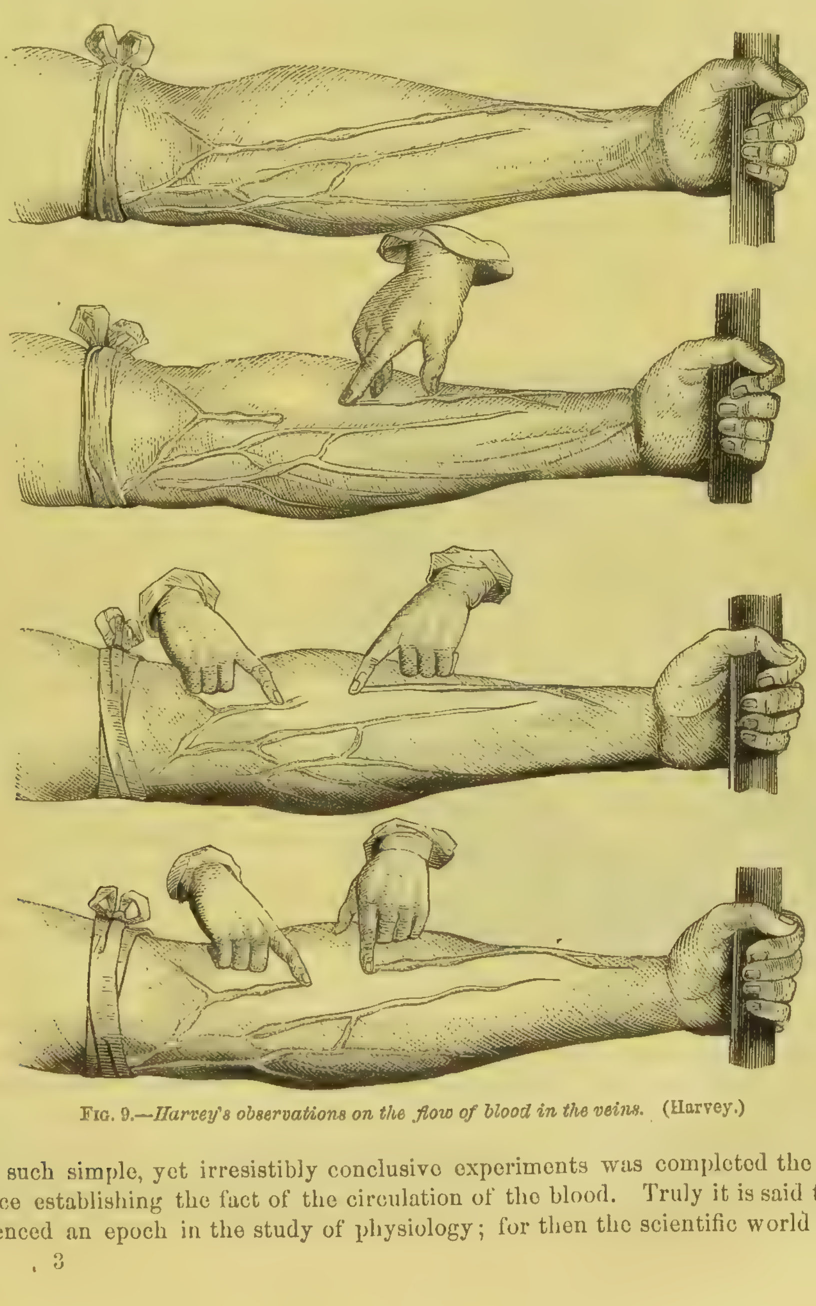


FIG. 9.—*Harvey's observations on the flow of blood in the veins.* (Harvey.)

By such simple, yet irresistibly conclusive experiments was completed the chain of evidence establishing the fact of the circulation of the blood. Truly it is said that here commenced an epoch in the study of physiology; for then the scientific world began to emancipate itself from the ideas of the ancients, which had held despotic sway for two centuries, and to study Nature for themselves by means of experiments.

Although Harvey described so perfectly the course of the blood and left not a shadow of doubt as to the communication between the arteries and veins, it was left to others to actually see the blood in movement and follow it from one system of vessels to the other. In 1661, Malpighi saw the blood circulating in the vessels of the lung of a living frog, examining it with magnifying glasses; and, a little later, Leeuwenhoek saw the circulation in the wing of a bat. The great discovery was then completed.

Enough has been said in the preceding historical sketch to give a general idea of the course of the great nutritive fluid and the natural anatomical and physiological divisions of the circulatory system. There is a constant flow from the central organ to all the tissues and organs of the body, and a constant return of the blood after it has passed through these parts. But before the blood, which has thus been brought back, is fit to return again to the system, it must pass through the lungs and undergo the changes incident to respiration. In some animals, like fishes, the same force sends the blood through the gills, and from them through the system. In others, like the reptiles, a mixture of aërated and non-aërated blood takes place in the heart, and the general system never receives blood that has been fully arterialized. But in man and all warm-blooded animals, the organism demands blood that has been fully purified and oxygenated by its passage through the lungs, and here we find the first great and complete divisions of the circulation into the pulmonary and systemic, or, as they have been called, the lesser and greater circulation. The heart in this instance is double; having a right and left side which are entirely distinct from each other. The right heart receives the blood as it is brought from the system by the veins and sends it to the lungs; the left heart receives the blood from the lungs and sends it to the system. It must be borne in mind, however, that although the two sides of the heart are distinct from each other, their action is simultaneous; and, in studying the motions of this organ, we shall find that the blood is sent simultaneously from the right side to the lungs, and from the left side to the system. It will not be necessary, therefore, to separate the two circulations in our study of their mechanism; for the simultaneous action of both sides of the heart enables us to study its functions as a single organ, and the constitution and operations of the two kinds of vessels do not present any material differences.

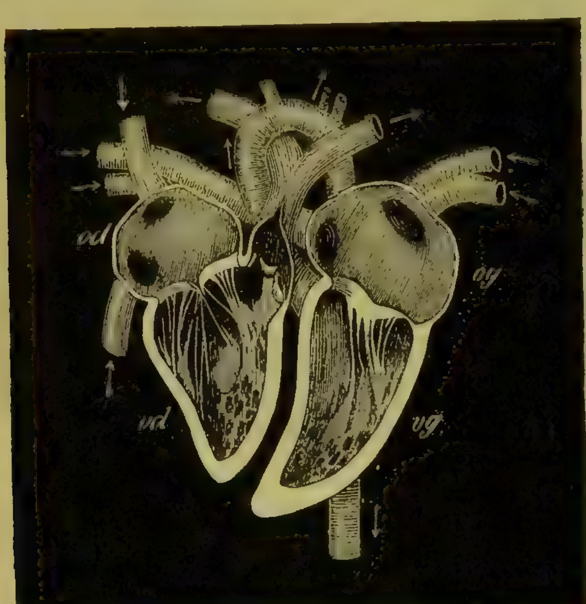


FIG. 10.—*Diagram of the four cavities of the heart.* (Bernard.) *od*, right auricle; *vd*, right ventricle; *og*, left auricle, *vg*, left ventricle. The arrows indicate the course of the blood.

For convenience of study, the circulatory system may be divided into heart and vessels, the latter being of three kinds: the arteries, which carry blood from the heart to the system; the capillaries, which distribute the blood more or less abundantly in different parts of the system; and the veins, which return the blood from the system to the heart. The functions of each of these divisions may be considered separately.

Physiological Anatomy of the Heart.

The heart of the human subject is a pear-shaped, muscular organ, situated in the thoracic cavity, with its base about in the median line and its apex at the fifth intercostal space midway between the median line and a perpendicular dropped through the left nipple. Its weight is from eight to ten ounces in the female, and from ten to twelve ounces in the male. It has four distinct cavities; a right and a left auricle, and a right and a left ventricle. Of these, the ventricles are the more capacious. The heart is held in place, or may be said to be attached by the great vessels to the posterior wall of the thorax, while the apex is free and capable of a certain degree of motion. The whole organ is enveloped in a fibrous sac called the pericardium. This sac is lined by a serous membrane, which is attached to the great vessels at the base and reflected over its surface. The membrane is lubricated by a drachm or two of fluid, so that the movements of the heart are normally accomplished without any friction. The serous pericardium does not present any differences from serous membranes in other situations. The cavities of the heart are lined by a smooth membrane, called the endocardium, which is continuous with the lining membrane of the blood-vessels.

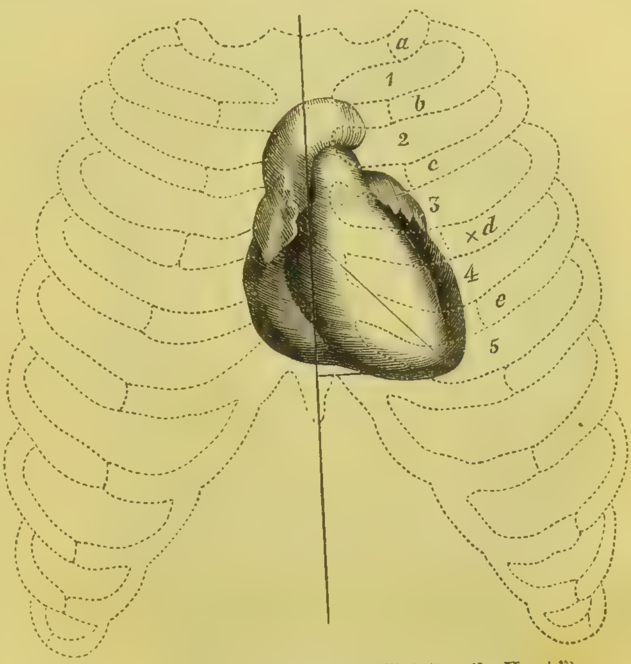


FIG. 11.—Heart *in situ*. (Dalton, in Flint, "on the Heart.")
a, b, c, etc., ribs; 1, 2, 3, etc., intercostal spaces; vertical line, median line; triangle, superficial cardiac region; × on the fourth rib, nipple.

The right auricle receives the blood from the venæ cavæ and empties it into the right ventricle. The auricle presents a principal cavity, or sinus, as it is called, with a little appendix, called from its resemblance to the ear of a dog, the auricular appendix. It has two large openings for the vena cava ascendens and the vena cava descendens, with a small opening for the coronary vein which brings the blood from the substance of the heart itself. It has, also, another large opening, called the auriculo-ventricular opening, by which the blood flows into the ventricle. The walls of this cavity are quite thin as compared with the ventricles, measuring about one line. They are composed of muscular fibres arranged in two layers, one of which, the external, is common to both auricles, and the other, the internal, is proper to each. These muscular fibres, although involuntary in their action, belong to the striated, or what is termed voluntary variety, and are similar in structure to the fibres of the ventricles. The fibres of the auricles are much fewer than those of the ventricles. Some of them are looped, arising from a cartilaginous ring which separates the auricles and ventricles, and passing over the auricles; and others are circular, surrounding the auricular appendages and the openings of the veins, extending, also, a short distance along the course of these vessels. One or two valvular folds are found at the orifice of the coronary vein, preventing a reflux of blood, but there are no valves at the orifices of the venæ cavæ.

The left auricle receives the blood which comes from the lungs by the pulmonary veins. It does not differ materially in its anatomy from the right. It is a little smaller, and its walls are thicker, measuring about a line and a half. It has four openings by which it receives the blood from the four pulmonary veins. These openings are not provided with valves. Like the right auricle, it has a large opening by which blood flows into the left ventricle. The arrangement of the muscular fibres is essentially the same as in the right auricle. In adult life, the cavities of the auricles are entirely distinct from each other. Before birth, they communicate by a large opening, the foramen ovale, and the orifice of the inferior vena cava is provided with a membranous fold, the Eustachian valve, which serves to direct the blood from the lower part of the body through the opening into the left auricle. After birth, the foramen ovale is closed and the Eustachian valve gradually disappears.

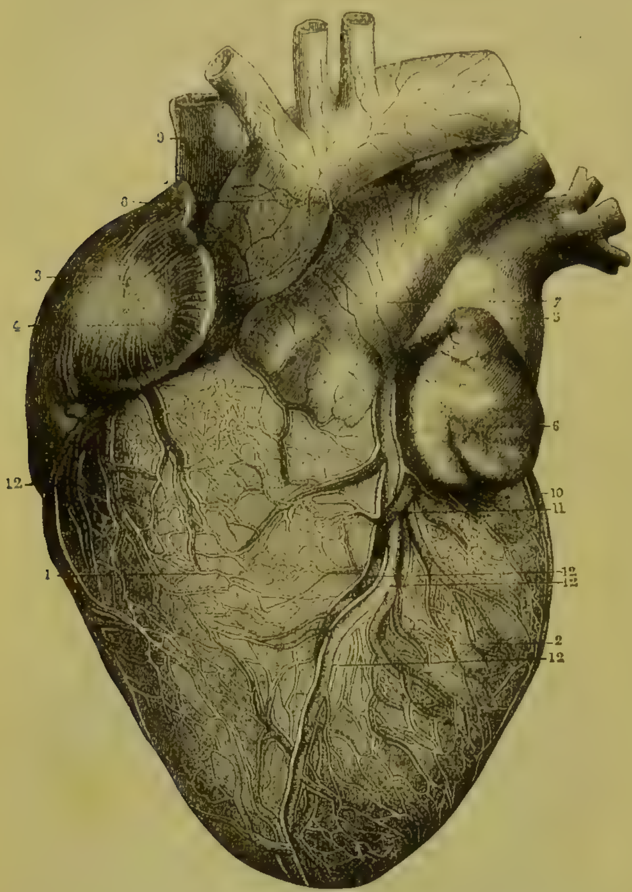


Fig. 12.—*Heart, anterior view.* (Bonamy and Beau.)
1, *right ventricle;* 2, *left ventricle;* 3, 4, *right auricle;* 5, 6, *left auricle;* 7, pulmonary artery; 8, aorta; 9, superior vena cava; 10, anterior coronary artery; 11, branch of the coronary vein; 12, 12, 12, lymphatic vessels.

The ventricles, in the human subject and in warm-blooded animals, constitute the bulk of the heart. They have a capacity somewhat greater than that of the auricles and are provided with thick muscular walls. It is by the powerful action of this portion of the heart that the blood is forced, on the one hand, to the lungs and back to the left side, and on the other, through the entire system of the greater circulation to the right side. It has been asserted that the capacity of the right ventricle is considerably greater than that of the left. The most recent and conclusive observations on this subject are those of Hiffelsheim and Robin. In these experiments, the cavities were filled with an injection of wax, and the estimates were made by calculating the amount of liquid displaced by the moulds of the different cavities. Care was taken to make the injection in animals before cadaveric rigidity had set in, or after it had passed away, in the human subject. The comparative results obtained by these observers are the most interesting, for the cavities were undoubtedly distended by the injection to their extreme capacity, and contained more than they ever do during life. They found the capacity of the right auricle from one-tenth to one-eighth greater than that of the left. The capacity of the right ventricle was from one-tenth to one-eighth greater than that of the left, but more frequently there was less disparity between the two ventricles than between the auricles. The capacity of each ventricle exceeded that of the corresponding auricle by from one-fourth to one-third. Nine times out of ten, this predominance of the ventricle was more marked on the left side. The absolute capacity of the left ventricle, according to these observations, is from 143 to 212 cubic centimeters, or from about 4·8 to 7 ounces. This is much greater than most estimates, which place the capacity of the various cavities, moderately distended, at about 2 ounces.

Notwithstanding the disparity in the extreme capacity of the various cavities, the quantity of blood which enters these cavities is necessarily equal to that which is expelled. This has been stated to be a little more than two ounces. There are no means of estimating with exactness the quantity of blood discharged with each ventricular contraction; and we find the question rather avoided in works on physiology. All we can say is that, from observations on the heart during its action, it never seems to contain much more than half the quantity in all its cavities that it does when fully distended by injection; but it is the right cavities which are most dilatable, and probably the ordinary quantity of blood in the left ventricle is from four-fifths to five-sixths of its extreme capacity.

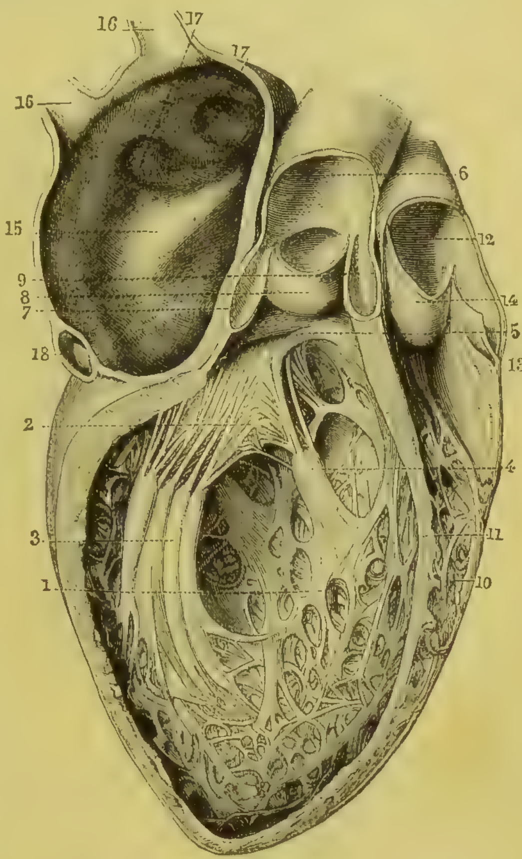


FIG. 13.—*Left cavities of the heart.* (Bonamy and Beau.) 1, *left ventricular cavity;* 2, *mitral valve;* 3, 4, *columnæ carneæ;* 5, *aortic opening;* 6, *aorta;* 7, 8, 9, *aortic valves;* 10, right ventricular cavity; 11, interventricular septum; 12, pulmonary artery; 13, 14, pulmonic valves; 15, left auricular cavity; 16, 16, right pulmonary veins, with 17, 17, openings of the veins; 18, section of the coronary vein.

The cavities of the ventricles are triangular or conoidal, the right being broader and shorter than the left, which extends to the apex. The inner surface of both cavities is marked by peculiar ridges and papillæ, which are called columnæ carneæ. Some of these are mere fleshy ridges projecting into the cavity; others are columns attached by each extremity and free at the central portion; and others are papillæ giving origin to the chordæ tendineæ, which are attached to the free edges of the auriculo-ventricular valves. These fleshy columns interlace in every direction and give the inner surface of the cavities a reticulated appearance. This arrangement evidently facilitates the complete emptying of the ventricles during their contraction.

The walls of the left ventricle are uniformly much thicker than on the right side. Bouillaud found the average thickness of the right ventricle at the base to be two and a half lines, and the thickness of the left ventricle at the corresponding part, seven lines.

The arrangement of the muscular fibres constituting the walls of the ventricles is more regular than in the auricles, and their course enables us to explain some of the phenomena which accompany the heart's action. The direction of the fibres cannot be well made out unless the heart have been boiled for a number of hours, when part of the intermuscular tissue is dissolved out, and the fibres can be easily separated and followed. Without going into a minute description of their direction, it is sufficient to state, in this connection, that they present two principal layers; a superficial layer common to both ventricles, and a deep layer proper to each. The superficial fibres pass obliquely from right to left from the base to the apex; here they take a spiral course, become deep, and pass into the interior of the organ to form the columnæ carneæ.

These fibres envelop both ventricles. They may be said to arise from cartilaginous rings which surround the auriculo-ventricular orifices. The external surface of the heart is marked by a little groove which indicates the division between the two ventricles. The deep fibres are circular, or transverse, and surround each ventricle separately.

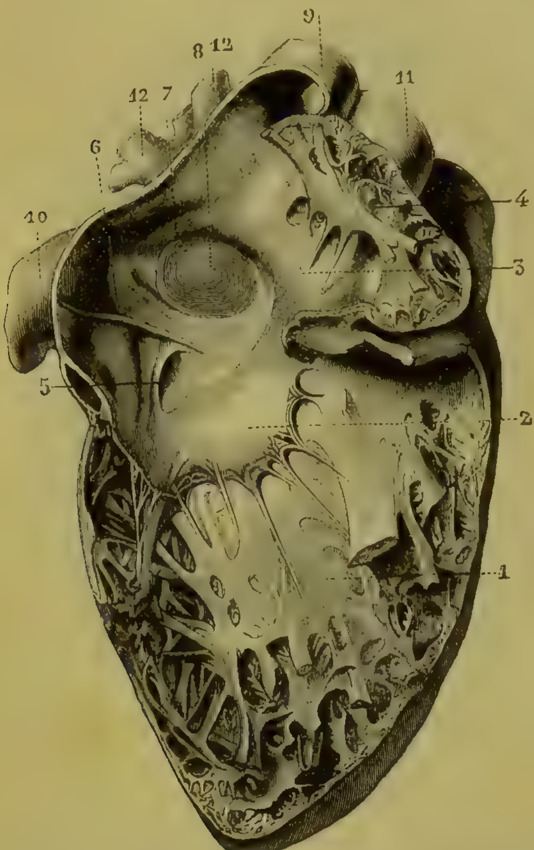


FIG. 14.—*Right cavities of the heart.* (Bonamy and Beau.) 1, *right ventricular cavity*; 2, *posterior curtain of the tricuspid valve*; 3, *right auricular cavity*; 4, *columnæ carneæ of the right auricle*; 5, section of the coronary vein; 6, Eustachian valve; 7, ring of Vieussens; 8, fossa ovalis; 9, superior vena cava; 10, inferior vena cava; 11, aorta; 12, 12, right pulmonary veins.

The muscular tissue of the heart is of a deep-red color and resembles, in its gross characters, the tissue of ordinary voluntary muscles; but, as already intimated, it presents certain peculiarities in its minute anatomy. The fibres are considerably smaller and more granular than those of ordinary muscles. They are, moreover, connected with each other by short inosculating branches, while in the voluntary muscles each fibre runs from its origin to its insertion enveloped in its proper sheath, or sarcolemma. The muscular fibres of the heart have no sarcolemma. These peculiarities, particularly the inosculation of the fibres, favor the contraction of the ventricular walls in every direction and the complete expulsion of the contents of the cavities with each systole.

The distribution of the nerves to the heart and the arrangement of the ganglia and nerve-terminations in its substance will be taken up in connection with the influence of the nervous system upon he action of the heart.

Each ventricle has two orifices; one by which it receives the blood from the auricle, and the other by which the blood passes from the right side to the lungs and from the left side to the system. All of these openings are provided with valves, which are so arranged as to allow the blood to pass in but one direction.

Tricuspid Valve.—This valve is situated at the right auriculo-ventricular opening. It has three curtains, formed of a thin but resisting membrane, which are attached around the opening. The free borders are attached to the chordæ tendineæ, some of which arise from the papillæ on the inner surface of the ventricle, and others, directly from the walls of the ventricle. When the organ is empty, these curtains are applied to the walls of the ventricle, leaving the auriculo-ventricular opening free; but when the ventricle is completely filled and the fibres contract, they are forced up, their free edges become applied to each other, and the opening is closed.

Pulmonic Valves.—These valves, also called the semilunar or sigmoid valves of the right side, are situated at the orifice of the pulmonary artery. They are strong membranous pouches, with their convexities, when closed, looking toward the ventricle. They are attached around the orifice of the pulmonary artery and are applied very nearly to the walls of the vessel when the blood passes in from the ventricle; but at other times their free edges meet in the centre, opposing the regurgitation of blood. At the centre of the free edge of each valve is a little corpuscle called the corpuscle of

Arantius; and, just above the margins of attachment of the valves, the artery presents three little dilatations, or sinuses, called the sinuses of Valsalva. The corpuscles of Arantius probably aid in the adaptation of the valves to each other and in the effectual closure of the orifice.

Mitral Valve.—This valve, sometimes called the bicuspid, is situated at the left auriculo-ventricular orifice. It is called mitral from its resemblance, when open, to a bishop's mitre. It is attached to the edges of the opening, and its free borders are held in place, when closed, by the chordæ tendineæ of the left side. It presents no material difference from the tricuspid valve, with the exception that it is divided into two curtains instead of three.

Aortic Valves.—These valves, also called the semilunar or sigmoid valves of the left side, present no difference from the valves at the orifice of the pulmonary artery. They are situated at the aortic orifice.

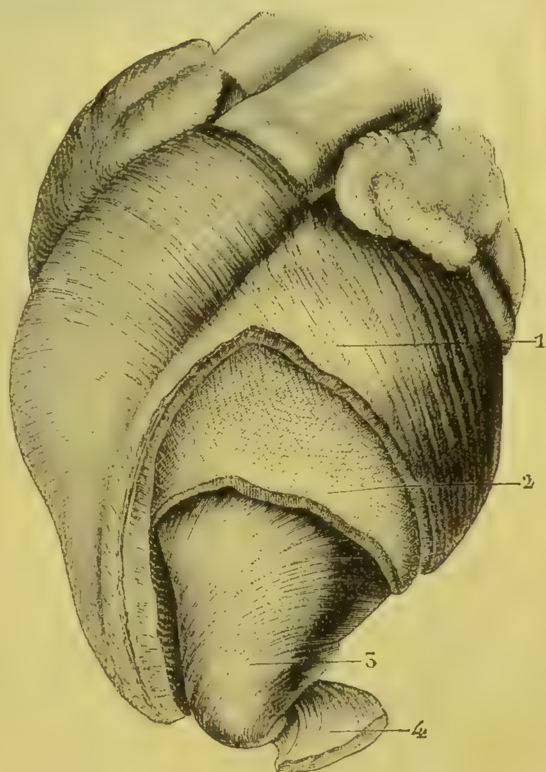


FIG. 15.—*Muscular fibres of the ventricles.* (Bonamy and Beau.) 1, superficial fibres, common to both ventricles; 2, fibres of the left ventricle; 3, deep fibres, passing upward toward the base of the heart; 4, fibres penetrating the left ventricle.

The physiological anatomy of the tricuspid and mitral valves may be studied by cutting away the auricles so as to expose the auriculo-ventricular openings, introducing a pipe into the pulmonary artery and aorta, after destroying the semilunar valves, and then forcing water into the ventricles by a syringe or from a hydrant. In this way the play of the valves may be strikingly exhibited.

We can study the action of the semilunar valves by cutting away enough of the ventricles to expose them and forcing water into the vessels. These experiments give an idea of the immense strength of the valves; for they can hardly be ruptured by a force which is not sufficient to rupture the vessels themselves.

FIG. 16.—*Anastomosing muscular fibres of the heart.* (Morel.)

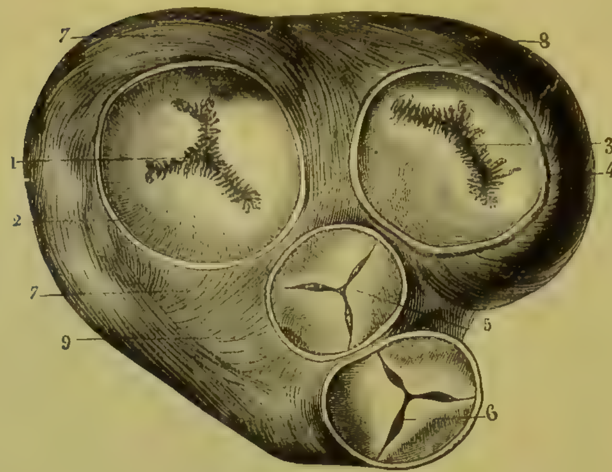


Fig. 17.—*Valves of the heart.* (Bonamy and Beau.)

1, Right auriculo-ventricular orifice, closed by the tricuspid valve; 2, fibrinous ring; 3, left auriculo-ventricular orifice, closed by the mitral valve; 4, fibrinous ring; 5, aortic orifice and valves; 6, pulmonic orifice and valves; 7, 8, 9, muscular fibres.

Movements of the Heart.

In studying the phenomena which accompany the action of the heart, we shall follow the course of the blood, beginning with it as it flows from the vessels into the auricles. The dilatation of the cavities of the heart is called the diastole, and the contraction of the heart, the systole. When these terms are used without any qualification, they are understood as referring to the ventricles; but they are also applied to the action of the auricles, as the auricular diastole or systole, which, as we shall see, is distinct from the action of the ventricles.

A complete revolution of the heart consists in the filling and emptying of all its cavities, during which they experience an alternation of repose and activity. As these phenomena occupy, in many warm-blooded animals, a period of time less than one second, it will be appreciated that the most careful study is necessary in order to ascertain their exact relations to each other. When the heart is exposed in a living animal, the most prominent phenomenon is the alternate contraction and relaxation of the ventricles; but this is only one of the operations of the organ. In all the mammalia, the anatomy and action of the vascular system are to all intents and purposes the same as in the human subject; and, although the exposure of the heart by opening the chest modifies somewhat the force and frequency of its pulsations, the various phenomena follow each other in their natural order and present essentially their normal characters. The operation of exposure of the heart may be performed on a living animal without any great difficulty; and, if we simply take care to keep up artificial respiration, the action of the heart will continue for a considerable time. We may keep the animal quiet by the administration of ether or by poisoning with woorara, the latter agent acting upon the motor nerves but having no effect upon the heart. Having opened the chest, we see the heart, enveloped in its pericardium, contracting regularly; and, on slitting up and removing this covering, the various parts are completely exposed. The right ventricle and auricle and a portion of the left ventricle can be seen without disturbing the position of the parts; but the greater part of the left auricle is concealed. As both auricles and ventricles act together, the parts of the heart which are exposed are sufficient for purposes of study.

Action of the Auricles.—Except the short time occupied in the contraction of the auricles, these cavities are continually receiving blood on the right side from the system, by the venæ cavæ, and on the left side from the lungs, by the pulmonary veins. This continues until the cavities of the auricles are completety filled, the blood coming in by a steady current; and, during the repose of the heart, the blood is also flowing through the auriculo-ventricular orifices into the ventricles. When the auricles have become fully distended, they contract quickly and with considerable power (the auricular systole), and force the blood into the ventricles, producing complete diastole of these cavities. During this contraction, the blood not only ceases to flow in from the veins, but some of it is regurgitated, as the orifices by which the vessels open into the auricles are not provided with valves. The size of the auriculo-ventricular orifices is one reason why the greater portion of the blood is made to pass into the ventricles; and, farthermore, during the auricular systole, the muscular fibres which are arranged around the orifices of the veins constrict them to a certain extent, which tends to diminish the reflux of blood. There can be no doubt that some regurgitation takes place from the auricles into the veins, but this prevents the possibility of over-distention of the ventricles.

It has been shown by experiments that the systole of the auricles is not immediately necessary to the performance of the circulation; and the contractility of the auricles may be temporarily exhausted by prolonged irritation, the ventricles continuing to act, keeping up the circulation of blood.

Action of the Ventricles.—Immediately following the contraction of the auricles, by which the ventricles are completely distended, we have contraction of the ventricles. This is the chief active operation performed by the heart and is generally spoken of as the systole. As we should expect from the great thickness of the muscular walls, the contraction of the ventricles is very much more powerful than that of the auricles. By their action, the blood is forced from the right side to the lungs by the pulmonary artery, and from the left side to the system by the aorta. Regurgitation into the auricles is prevented by the closure of the tricuspid and mitral valves. This act accomplished, the heart has a period of repose, the blood flowing into the auricles, and from them into the ventricles, until the auricles are filled and another contraction takes place.

Locomotion of the Heart.—The position of the heart after death or during the repose of the organ is with its base directed slightly to the right and its apex to the left side of the body. With each ventricular systole, it raises itself up, the apex is sent forward, and is moved slightly from left to right. The movement from left to right is a necessary consequence of the course of the superficial fibres. The fibres on the anterior surface of the organ are longer than those on the posterior surface, and pass from the base, which is comparatively fixed, to the apex, which is movable. As a consequence of this anatomical arrangement, the heart is moved upward and forward during its systole. The course of the fibres from the base to the apex is from right to left; and, as they shorten, the apex is of necessity slightly moved from left to right.

The locomotion of the entire heart forward was observed by Harvey, in the case of the son of the Viscount Montgomery. The young man, aged about nineteen years, suffered a severe injury to the chest, resulting in an abscess, which on cicatrization left an opening into which Harvey could introduce three fingers and the thumb. This opening was directly over the apex of the heart. The action of the portion of the heart thus exposed is described by Harvey in the following words:

"We also particularly observed the movements of the heart, viz.: that in the diastole it was retracted and withdrawn; whilst in the systole it emerged and protruded; and the systole of the heart took place at the moment the diastole or pulse in the wrist was perceived. To conclude, the heart struck the walls of the chest, and became prominent at the time it bounded upward and underwent contraction on itself."

The locomotion of the heart takes place in the direction of its axis and is due to the sudden distention of the great vessels at its base. These vessels are eminently elastic, and, as they receive the charge of blood from the ventricles, become enlarged in every direction and consequently project the entire organ against the walls of the chest. This movement is aided by the recoil of the ventricles as they discharge their contents. The displacement of the heart during its systole has long been observed in vivisections and may be demonstrated in any of the mammals. The most interesting observations on this point are those of Chauveau and Faivre, which were made upon a monkey. In this animal, in which the position of the heart is very much the same as in the human subject, the locomotion of the organ was fully established.

Twisting of the Heart.—The spiral course of the superficial fibres would lead us to look for another phenomenon accompanying its contraction; namely, twisting. If we attentively watch the apex of the heart, especially when its action has become a little retarded, there is a palpable twisting of the point upon itself from left to right with the systole, and an untwisting with the diastole.

Hardening of the Heart.—If the heart of a living animal be grasped by the hand, it will be observed that at each systole it becomes hardened. The fact that it is composed almost exclusively of fibres, resembling very closely those of the voluntary muscles, explains this phenomenon. Like any other muscle, it is sensibly hardened during contraction.

Shortening and Elongation of the Heart.—The phenomena which we have just described are admitted by all writers on physiology and can easily be observed; but the change in length of the heart during its systole has been a matter of discussion. All who have studied the heart in action have observed changes in length during contraction and relaxation; but the contemporaries of Harvey were divided as to the periods in the heart's action which are attended with elongation and shortening. Harvey himself is not absolutely definite on this point. In one passage he says, in describing the systole, "that it is everywhere contracted, but especially towards the sides, so that it looks narrower, a little longer, more drawn together." In his description of the case of the son of the Viscount Montgomery, who suffered from ectopia cordis, he states that during the systole the heart "emerged and protruded." Vesalius, Fontana, and some others, contended for elongation during the systole; but Haller, Steno, Lancisi, and Bassuel stated that it becomes shortened. The view generally entertained at the present day is that the heart is shortened during its systole. There is no doubt that the point of the heart is protruded during the ventricular systole, but this protrusion is not due to elongation of the ventricles. By suddenly cutting the heart out of a warm-blooded animal and watching the phenomena which accompany the few regular contractions which follow, it is seen that the ventricles invariably shorten during the systole. This can easily be appreciated by the eye, but more readily if the point of the organ be brought just in contact with a plane surface at right angles, when, at each contraction, it is unmistakably observed to recede. The following experiments we have frequently repeated before the class of the Bellevue Hospital Medical College, and have satisfied ourselves of their accuracy. A large Newfoundland pup, about nine months old, was poisoned with woorara, artificial respiration was kept up, and the heart exposed. After showing the protrusion of the point and the apparent elongation of the heart while in the chest, the organ was rapidly removed, placed upon the table, and confined by two long needles passed through the base, pinning it to the wood. It contracted for one or two minutes, and at each systole the ventricles were manifestly shortened. The point was then placed against an upright, and it receded with each systole about an eighth of an inch. This phenomenon was apparent to all present. In another experiment, performed a few weeks later, the heart, which had been exposed in the same way, was examined *in situ*, by pinning it with two needles to a thin board passed under the organ. The presence of the needles did not seem to interfere with the heart's action, and, at each ventricular systole, the point evidently approached the base. To render this absolutely certain, a knife was fixed in the wood at right angles to and touching the point during the diastole, and a small silver tube was introduced through the walls into the left ventricle. At each contraction, a jet of blood spurted out through the tube, and the point of the heart receded from the knife about an eighth of an inch. The animal experimented upon was a dog a little above the medium size. These simple experiments demonstrate that, in the dog at least, the ventricles shorten during their systole. The arrangement of the muscular fibres is too nearly identical in the heart of the warm-blooded animals to leave room for doubt that it also shortens in the human subject. The error which has arisen in this respect, and which obtained in our first experiments made in 1861, is due to the locomotion and protrusion of the entire organ, so as to make the point strike against the chest. A little reflection indicates the mechanism of this phenomenon. During the intervals of contraction, the great vessels, particularly the aorta and pulmonary artery, which attach the base of the heart to the posterior wall of the thorax, are filled but not distended with blood; at each systole, however, these vessels are distended to their utmost capacity; their elastic coats permit of considerable enlargement, as can be seen in the living animal, and this enlargement, taking place in every direction, pushes the whole organ forward. We have also considerable locomotion of the heart from recoil. It is for this reason that, observing the heart *in situ*, the ventricles seem to elongate. It is only when we examine the heart firmly fixed, or contracting after it is removed from the body, that we can appreciate the actual changes which occur in the length of the ventricles. During the systole the ventricles are shortened and are narrowed in their transverse diameter, but their antero-posterior diameter is slightly increased.

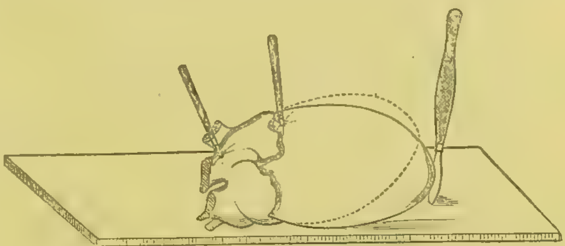


FIG. 18.—*Diagram of the shortening of the ventricles during systole.*
The dotted lines show the position of the heart during contraction.

In addition to the marked changes in form, position, etc., which the heart undergoes during its action, we observe, on careful examination, that the surface of the ventricles becomes marked with slight longitudinal ridges during the systole. This was not noted by Harvey but is mentioned by Haller.

Impulse of the Heart.—Each movement of the heart produces an impulse, which can be readily felt and sometimes seen, in the fifth intercostal space, a little to the left of the median line. Vivisections have demonstrated that the impulse is synchronous with the contraction of the ventricles. If the hand be introduced into the chest of a living animal, and the finger be placed between the point of the heart and the walls of the thorax, every time that we have a hardening of the point, the finger will be pressed against the side. If the impulse of the heart be felt while the finger is on the pulse, it is evident that the heart strikes against the thorax at the time of the distention of the arterial system. The impulse is due to the locomotion of the ventricles. In the words of Harvey, "the heart is erected, and rises upwards to a point, so that at this time it strikes against the breast and the pulse is felt externally." In the case of the son of the Viscount Montgomery, already referred to, Harvey gives a most graphic description of the manner in which the heart is "retracted and withdrawn" during the diastole, and "emerged and protruded" during the systole.

Succession of the Movements of the Heart.—We have already followed, in a general way, the course of the blood through the heart and the successive action of the various parts; but we have yet to consider these points more in detail, and to ascertain, if possible, the relative periods of activity and repose in each portion of the organ.

The great points in the succession of movements are readily observed in the hearts of cold-blooded animals, in which the pulsations are very slow. In examining the heart of the frog, turtle, or alligator, the alternations of repose and activity are very strongly marked. During the intervals of contraction, the whole heart is flaccid, and the ventricle is comparatively pale; we then see the auricles slowly filling with blood; when they have become fully distended, they contract and fill the ventricle, which, in these animals, is single; the ventricle immediately contracts, its action following upon the contraction of the auricles as if it were propagated from them. When the heart is filled with blood, it has a dark-red color, which contrasts strongly with its appearance after the systole. This operation may occupy from ten to twenty seconds, giving an abundance of time for observation. The case is different, however, with the warm-blooded animals, in which the anatomy of the heart is nearly the same as in man. Here a normal revolution may occupy less than a second; and it is evident that the varied phenomena we have just mentioned are followed with the utmost difficulty. In spite of this rapidity of action, it can be seen that a rapid contraction of the auricles precedes the ventricular systole, and that the latter is synchronous with the impulse.

Various estimates have been made of the relative time occupied by the auricular and ventricular contractions; and the question has been at last definitely settled by the observations of Marey, who has constructed very ingenious and delicate instruments for registering the form and frequency of the pulse. He devised a series of most interesting experiments, in which he was enabled to register simultaneously the pulsations of the different divisions of the heart, and has succeeded in establishing a definite relation between the contractions of the auricles and ventricles. The method of Marey enables us to determine, to a small fraction of a second, the duration of the contraction of each of the divisions of the heart.

The method of transmitting the movement from the heart to a registering apparatus is very simple. The apparatus consists of two little elastic bags connected together by an elastic tube, the whole closed and filled with air. A pressure, like the pressure of the fingers, upon one of these bags produces, of course, an instantaneous and corresponding dilatation of the other. If we suppose one of these bags to be introduced into one of the cavities of the heart, and the other placed under a small lever arranged on a pivot so as to be sensible to the slightest impression, it is evident that any compression of the bag in the heart would produce a corresponding change in volume in the other bag, which would be indicated by a movement of the lever. Marey arranged the lever with its short arm on the elastic bag, and the long arm, provided with a pen, moving against a roll of paper, which passes along at a uniform rate. When the lever is at rest with the paper set in motion, the pen will make a horizontal mark; but when the lever ascends and descends, a corresponding trace will be made, and the duration of any movement can readily be estimated by calculating the rapidity of the motion of the paper. The bag which receives the impression is called by Marey the initial bag, and the other, which is connected with the lever, is called the terminal bag. The former may be modified in form with reference to the situation in which it is to be placed.

The experiments of M. Marey, with reference to the relations between the systole of the auricles, the systole of the ventricles, and the impulse of the heart, were performed upon horses, in the following way:

A sound is introduced into the right side of the heart through the jugular vein, an operation which may be performed with certainty and ease. This sound is provided with two initial bags, one of which is lodged in the right auricle, while the other passes into the ventricle. The bags are connected with distinct tubes which pass one within the other, and are connected by elastic tubing with the registering apparatus. At each systole of the heart, the bags in its cavities are compressed and produce corresponding movements of the levers, which may be registered simultaneously.

To register the impulse of the heart, an incision is made through the skin and the external intercostal muscle over the point where the apex-beat is felt. A little bag, stretched over two metallic buttons separated by a central rod, is then carefully secured in the cavity thus formed, and connected by an elastic tube with the registering apparatus. All the tubes are provided with stop-cocks, so that each initial bag may be made to communicate with its lever at will. When the operation is concluded and the sound firmly secured in place by a ligature around the vein, the animal experiences no inconvenience, is able to walk about, eat, etc., and there is every evidence that the circulation is not interfered with. The cylinders which carry the paper destined to receive the traces are arranged to move by clock-work at a given rate. The paper may also be ruled in lines, the distances between which represent certain fractions of a second. Fig. 19 represents the apparatus reduced to one-sixth of its actual size. Two of the levers are connected

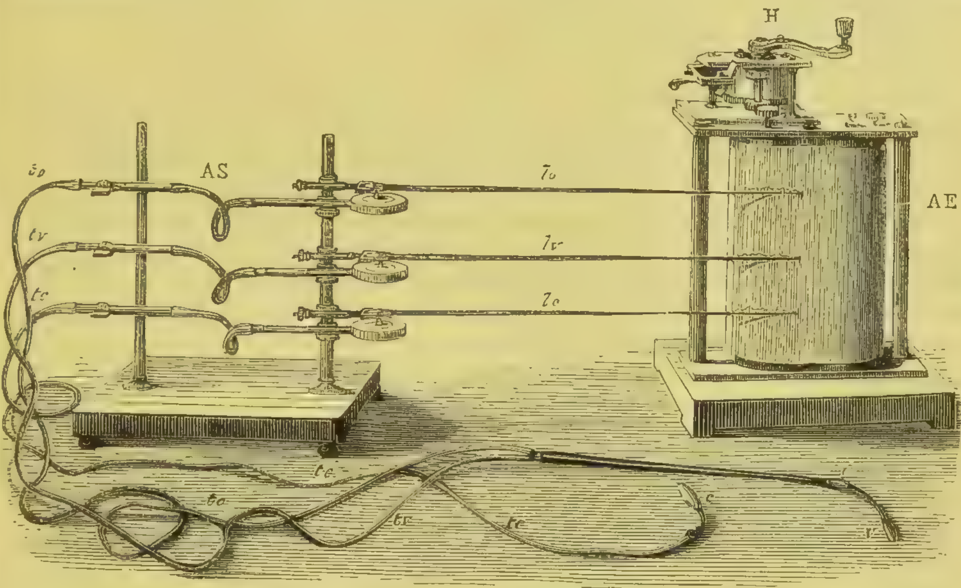


Fig. 19.—*Cardiograph.* (Chauveau and Marey.)

"The instrument is composed of two principal elements: A E, the registering apparatus, and A S, the sphygmographic apparatus, that is to say, which receives, transmits, and amplifies the movements which are to be studied." The compression exerted upon the bag *c*, which is placed over the apex of the heart between the intercostal muscles, is conducted by the tube *tc*, which is filled with air, to the first lever. The compression exerted upon the bags *o* and *v*, in the double sound, is conducted by the tubes *to* and *tv* to the two remaining levers. The movements of the levers are registered simultaneously by the cylinders A E.

with the double sound for the right auricle and ventricle, and one is connected with the bag destined to receive the impulse of the heart. In an experiment upon a horse, every thing being carefully arranged in the way indicated, the clock-work was set in motion, and the movements of the three levers produced traces upon the paper which were interpreted as follows:

1. The paper was ruled so that each division represented one-tenth of a second. The traces formed by the three levers indicated four revolutions of the heart. The first revolution occupied $1\frac{1}{10}$ sec., the second, $1\frac{2}{10}$ sec., the third, $1\frac{1}{10}$ sec., and the fourth, 1 sec.

2. The auricular systole, as marked by the first lever, immediately preceded the ventricular systole, and occupied about two-tenths of a second. The elevation of the lever indicated that it was much more feeble than the ventricular systole, and sudden in its character; the contraction, when it had arrived at the maximum, being immediately followed by relaxation.

3. The ventricular systole, as marked by the second lever, immediately followed the auricular systole, and occupied about four-tenths of a second. The almost vertical direction of the trace and the degree of elevation showed that it was sudden and powerful in

its character. The abrupt descent of the lever showed that the relaxation was almost instantaneous.

4. The impulse of the heart, as marked by the third lever, was shown to be absolutely synchronous with the ventricular systole.

Condensing the general results obtained by Marey, which are of course subject to a certain amount of variation, we have, dividing the action of the heart into ten equal parts, three distinct periods, which occur in the following order:

Auricular Systole.—This occupies two-tenths of the heart's action. It is feeble as compared with the ventricular systole, and relaxation immediately follows the contraction.

Ventricular Systole.—This occupies four-tenths of the heart's action. The contraction is powerful and the relaxation, sudden. It is absolutely synchronous with the impulse of the heart.

Auricular Diastole.—This occupies four-tenths of the heart's action.

Force of the Heart.—There are few points in physiology concerning which opinions have been more widely divergent than the question of the force employed by the heart at each contraction. Borelli, who was the first to give a definite estimate of this force, put it at 180,000 pounds, while the calculations of Keill give only 5 ounces. These estimates, however, were made on purely theoretical grounds. Borelli estimated the force employed by the deltoid in sustaining a given weight held at arm's length, and formed his estimate of the power of the heart by comparing the weight of the organ with that of the deltoid. Keill made his estimate from a calculation of the rapidity of the current of blood in the arteries. Hales was the first to investigate the question experimentally, by the application of the cardiometer. He showed that the pressure of blood in the aorta could be measured by the height to which the fluid would rise in a tube connected with that vessel, and estimated the force of the left ventricle by multiplying the pressure in the aorta by the area of the internal surface of the ventricle. The cardiometer has undergone various improvements and modifications, but the above is the principle which is so extensively made use of at the present day in estimating the pressure of the blood in different parts of the circulatory system. First we have the improvement of Poiseuille, who substituted a U-tube partly filled with mercury for the long straight tube of Hales; and then, the various forms of cardiometers constructed by Magendie, Bernard, Marey, and others, which will be more fully discussed in connection with the arterial circulation. These instruments have been made use of by Marey, with very good results, in investigating the relative force exerted by the different divisions of the heart.

Hales estimated, from experiments upon living animals, the height to which the blood would rise in a tube connected with the aorta of the human subject, at 7 feet 6 inches, and gives the area of the left ventricle as 15 square inches. From this he calculates the force of the left ventricle as equal to 51·5 pounds. Although this estimate is only an approximation, it seems to be based on more reasonable data than any other.

The apparatus of Marey for registering the contractions of the different cavities of the heart enabled him to ascertain the comparative force of the two ventricles and the right auricle; the situation of the left auricle precluding the possibility of introducing a sound into its cavity. By first subjecting the bags to known degrees of pressure, the degree of elevation of a lever may be graduated so as to represent the degrees of the cardiometer. In analyzing traces made by the left ventricle, the right ventricle, and right auricle, in the horse, Marey found that, as a general rule, the comparative force of the right and left ventricles is as one to three. The force of the right auricle is comparatively insignificant, being in one case, as compared with the right ventricle, only as one to ten.

Action of the Valves.—We have already indicated the course of the blood through the cavities of the heart, and it has been apparent that the necessities of the circulation demand some arrangement by which the current shall always be in one direction. The anatomy of the valves which guard the orifices of the ventricles gives an idea of their function; but we have yet to consider the precise mechanism by which they are opened and closed and the way in which regurgitation is prevented.

In man and the warm-blooded animals, there are no valves at the orifices by which the veins open into the auricles. As has already been seen, compared with the ventricles, the force of the auricles is insignificant; and it has farthermore been shown by experiment that the ventricles may be filled with blood and the circulation continue, when the auricles are entirely passive. Although the orifices are not provided with valves, the circular arrangement of the fibres about the veins is such, that during the contraction of the auricles the openings are considerably narrowed, and regurgitation cannot take place to any great extent. The force of the blood flowing into the auricles likewise offers an obstacle to its return. There is really no valvular apparatus which operates to prevent regurgitation from the heart into the veins; for the valvular folds, which are so numerous in the general venous system, and particularly in the veins of the extremities, do not exist in the venæ cavæ. The continuous flow of blood from the veins into the auricles, the feeble character of the auricular contractions, the arrangement of the fibres around the orifices of the vessels, and the great size of the auriculo-ventricular openings, are conditions which provide sufficiently for the flow of blood into the ventricles.

Action of the Auriculo-Ventricular Valves.—After the ventricles have become completely distended by the auricular systole, they take on their contraction, which, it will be remembered, is very many times more powerful than the contraction of the auricles. They have to force open the valves which close the orifices of the pulmonary artery and aorta and empty their contents into these vessels. To accomplish this, at the moment of the ventricular systole, there is an instantaneous and complete closure of the auriculo-ventricular valves, leaving but one opening through which the blood can pass. That these valves close at the moment of contraction of the ventricles is demonstrated by the experiments of Chauveau and Faivre, who introduced the finger through an opening into the auricle and actually felt the valves close at the instant of the ventricular systole. This tactile demonstration, and the fact that the first sound of the heart, which is produced in great part by the closure of the auriculo-ventricular valves, is synchronous with the ventricular systole, leave no doubt as to the mechanism of the closure of these valves. It is probable that, as the blood flows into the ventricles, the valves are slightly floated out, but they are not closed until the ventricles contract.

If a bullock's heart be prepared by cutting away the auricles so as to expose the mitral and tricuspid valves, securing the nozzles of a double syringe in the pulmonary artery and aorta, after having destroyed the semilunar valves, and if fluid be injected simultaneously into both ventricles, the play of the valves will be exhibited. The mitral valve effectually prevents the passage of fluid, its edges being so accurately approximated that not a drop passes between them; but, when the pressure is considerable, a certain quantity of fluid passes the tricuspid valve. There is, indeed, a certain amount of insufficiency at the right auriculo-ventricular orifice, which does not exist on the opposite side.

The fact just noted was first pointed out by Mr. T. W. King, and is called by him the "safety-valve function of the right ventricle." The advantage of this slight insufficiency is apparent on a little reflection. The right ventricle sends its blood to the lungs, where, in order to facilitate the respiratory processes, the walls of the capillaries are very thin. The lungs themselves are exceedingly delicate, and an effusion of blood, or considerable congestion, would be liable to be followed by serious consequences. To prevent this, the right ventricle is not permitted to exert all its force, under all circumstances, upon the blood going into the pulmonary artery; but, when the action of the heart is exaggerated from any cause, the lungs are relieved by a slight regurgitation, which takes place through the tricuspid valve. The lungs are still farther protected by the sufficiency of the mitral valve, which effectually prevents regurgitation from the left ventricle. In the systemic circulation, the capillaries are less delicate; extravasation of blood would not be followed by any serious results; and the circulating fluid is made to pass through a considerable extent of elastic vessels, before it is distributed in the tissues. It is evident that, on the left side, there is no necessity for such a provision, and it does not exist.

Action of the Aortic and Pulmonic Valves.—The action of the semilunar valves is nearly the same upon both sides. In the intervals of the ventricular contractions, they are closed and prevent regurgitation of blood into the ventricles. The systole, however, overcomes the resistance of these valves and forces the contents of the ventricles into the arteries. During this time, the valves are applied, or nearly applied, to the walls of the vessel; but, so soon as the ventricles cease their contraction, the constant pressure of the blood, which, as we shall see hereafter, is very great, instantaneously closes the openings.

The action of the semilunar valves can be exhibited by cutting away a portion of the ventricles in the heart of a large animal, securing the nozzles of a double syringe in the aorta and pulmonary artery, and forcing water into the vessels. In performing this experiment, it will be noticed that, while the aortic semilunar valves oppose the passage of the liquid so effectually that the aorta may be ruptured before the valves will give way, a considerable degree of insufficiency exists, under a high pressure, at the orifice of the pulmonary artery. There is at this orifice a safety-valve function as important as that ascribed by King to the tricuspid valve. It is evident that the slight insufficiency at the pulmonic orifice may be even more directly important in protecting the lungs than the insufficiency of the tricuspid valve. The difference in the sufficiency of the semilunar valves on the two sides is fully as marked as between the auriculo-ventricular valves; and it is surprising that, since the observations of King, this fact, which we demonstrated for the first time in 1864, has not attracted the attention of physiologists.

It is probable that the corpuscles of Arantius, which are situated in the middle of each valvular curtain, assist in the accurate closure of the orifice. The sinuses of Valsalva, situated in the artery behind the valves, are regarded as facilitating the closure of the valves by allowing the blood to pass easily behind them.

Sounds of the Heart.—If the ear be applied to the præcordial region, it will be found that the action of the heart is accompanied by certain sounds. A careful study of these sounds and of their modifications in disease has enabled the practical physician to distinguish, to a certain extent, the conditions of the heart by auscultation. This increases the interest which attaches to the audible manifestations of the action of the great central organ of the circulation.

The appreciable phenomena which attend the heart's action are connected with the systole of the ventricles. It is this which produces the impulse against the walls of the thorax, and, as we shall see farther on, the dilatation of the arterial system, called the pulse. It is natural, therefore, in studying these phenomena, to take the systole as a point of departure, instead of the action of the auricles, which we cannot appreciate without vivisections; and the sounds, which are two in number, have been called first and second, with reference to the systole.

The first sound is absolutely synchronous with the apex-beat. The second sound follows the first with scarcely an appreciable interval. Between the second and the first sound, there is an interval of silence.

Some writers have attempted to represent the sounds of the heart and their relations to each other, by certain syllables, as, "*lubb-dup* or *lubb-tub;*" but it seems unnecessary to attempt to make such a comparison, which can only be appreciated by one who is practically acquainted with the heart-sounds, when the sounds themselves can be so easily studied.

Both sounds are generally heard with distinctness over any part of the præcordia. The first sound is heard with its maximum of intensity over the body of the heart, a little below and within the nipple, between the fourth and fifth ribs, and is propagated with greatest facility downward, toward the apex. The second sound is heard with its maximum of intensity at the base of the heart, between the nipple and the sternum, at about the locality of the third rib, and is propagated upward, along the course of the great vessels.

The rhythm of the sounds bears a certain relation to the rhythm of the heart's action, which we have already discussed; the difference being, that we here regard the heart's action as commencing with the systole of the ventricles, while, in following the action of different parts of the organ, we followed the course of the blood and commenced with the systole of the auricles. Laennec was the first to direct special attention to the rhythm of these sounds, although they had been recognized by Harvey, who compared them to the sounds made by the passage of fluids along the œsophagus of a horse when drinking. He divided a single revolution of the heart into four parts: the first two parts are occupied by the first sound; the third part, by the second sound; and in the fourth part there is no sound. He regarded the second sound as following immediately after the first. Some authors have described a "short silence" as occurring after the first sound, and a "long silence," after the second sound. The short silence, if appreciable at all, is so indistinct that it may practically be disregarded.

Most physiologists regard the duration of the first sound as a little less than two-fourths of the heart's action, and the second sound as a little more than one-fourth. When we come to consider the mechanism of the production of the two sounds, we shall see that, if our views on that point be correct, the first sound should occupy the period of the ventricular systole, or four-tenths of the heart's action, the second sound about three-tenths, and the repose three-tenths.

The first sound is relatively dull, low in pitch, and is made up of two elements; one, a valvular element, in which it resembles in character the second sound, and the other, an element which is due to the action of the heart as a muscle. It has been ascertained that all muscular contraction is attended with a certain sound. To this is added an impulsion element, which is produced by the striking of the heart against the walls of the thorax.

The second sound is relatively sharp, high in pitch, and has but one clear element, which we have already alluded to as valvular.

Causes of the Sounds of the Heart.—There is now scarcely any difference of opinion with regard to the cause of the second sound of the heart. The experiments of Rouanet, published in 1832, settled beyond a doubt that it is due to a closure of the aortic and pulmonary semilunar valves. In his essay upon this subject, Rouanet acknowledges his indebtedness for the first suggestion of this explanation to Mr. Carswell, who was at that time prosecuting his studies in Paris. The experiments by which this is demonstrated are as simple as they are conclusive. First we have the experiments of Rouanet, who imitated the second sound by producing sudden closure of the aortic valves by a column of water. We then have the experiments, even more conclusive, of the British Commission, in which the semilunar valves were caught up by curved hooks introduced through the vessels of a living animal, the ass, with the result of abolishing the second sound and substituting for it a hissing murmur. When the instruments were withdrawn and the valves permitted to resume their action, the normal sound returned.

It is unnecessary to discuss the various theories which have been advanced to explain the second sound, as it is now generally acknowledged to be due to the sudden closure of the semilunar valves at the orifices of the aorta and pulmonary artery. We remark, however, that the sound is heard with its maximum of intensity over the site of these valves, and is propagated along the great vessels, to which they are attached. It also occurs precisely at the time of their closure; viz., immediately following the ventricular systole.

The cause of the first sound of the heart has not, until within a few years, been so well understood. It was maintained by Rouanet that this sound was produced by the sudden closure of the auriculo-ventricular valves; but the situation of these valves rendered it difficult to demonstrate this by actual experiment. We have already seen, that, while the second sound is purely valvular in its character, the first sound is composed of a certain number of different elements; but auscultatory experiments have been made by which all but the valvular element are eliminated and the character of the first sound made to resemble that of the second. Conclusive observations on this point were made a few years ago by Dr. Austin Flint, constituting part of an essay which received the prize of the American Medical Association in 1858. In this essay, the following points were established:

1. If a folded handkerchief be placed between the stethoscope and integument, the first sound is divested of some of its most distinctive features. It loses the quality of impulsion and presents a well-marked valvular quality.

2. In many instances, when the stethoscope is applied to the præcordia while the subject is in a recumbent posture and the heart is removed by force of gravity from the anterior wall of the thorax, the first sound becomes purely valvular in character and as short as the second.

3. When the stethoscope is applied to the chest a little distance from the point where the first sound is heard with its maximum of intensity, it presents only its valvular element.

These observations, taken in connection with the fact that the first sound occurs when the ventricles contract and necessarily accompanies the closure of the auriculo-ventricular valves, show pretty conclusively that these valves produce at least one element of the sound. In farther support of this opinion, we have the fact that the first sound is heard with its maximum of intensity over the site of the valves and is propagated downward along the ventricles, to which the valves are attached. Actual experiments are not wanting to confirm this view. Chauveau and Faivre have succeeded in abolishing the first sound by the introduction of a wire ring into the auriculo-ventricular orifice through a little opening in the auricle, so as to prevent the closure of the valves. When this is done, the first sound is lost; but on taking it out of the opening the sound returns. These observers also abolished the first sound by introducing a small curved tenotomy-knife through the auriculo-ventricular orifice and dividing the chordæ tendineæ. In this experiment a loud rushing murmur took the place of the sound. These observations and experiments settle beyond question the fact that the closure of the auriculo-ventricular valves produces one element of the first sound.

The other elements which enter into the composition of the first sound are not so prominent as the one we have just considered, although they serve to give it its prolonged and "booming" character. These elements are, a sound like that produced by any large muscle during its contraction, called by some the muscular murmur, and the sound produced by the impulse of the heart against the walls of the chest.

There can be no doubt but that the muscular murmur is one of the elements of the first sound; and it is this which gives its prolonged character when the stethoscope is applied over the body of the organ, as the sound produced in muscles continues during the whole period of their contraction. Admitting this to be an element of the first sound, we can understand how its duration must necessarily coincide with that of the ventricular systole. We can appreciate, also, how all but the valvular element is eliminated when the stethoscope is moved from the body of the heart, the muscular sound not being propagated as completely as the sound made by the closure of the valves.

The impulse of the heart against the walls of the thorax also contributes to produce the first sound. This is demonstrated by noting the difference in the sound when the subject is lying upon the back, and when he is upright, by interposing any soft substance between the stethoscope and the chest, or by auscultating the heart after the sternum has been removed. Under these conditions, the first sound loses its booming character, retaining, however, the muscular element, when the instrument is applied to the exposed organ.

The first sound of the heart is complex. It is produced by the sudden closure of the auriculo-ventricular valves at the beginning of the ventricular systole, to which are superadded, the muscular sound, due to the contraction of the muscular fibres of the heart, and the impulsion-sound, due to the shock of the organ against the walls of the thorax.

The second sound is simple. It is produced by the sudden closure of the aortic and pulmonic semilunar valves, immediately following the ventricular systole.

It is of the greatest importance, with reference to pathology, to have a clear idea of the currents of blood through the heart, with their exact relation to the sounds and intervals. At the commencement of the first sound, the blood is forcibly thrown from the ventricles into the pulmonary artery on the right side and the aorta on the left, and the auriculo-ventricular valves are suddenly closed. During the entire period occupied by this sound, the blood is flowing rapidly through the arterial orifices, and the auricles are receiving blood slowly from the venæ cavæ and the pulmonary veins. When the second sound occurs, the ventricles having become suddenly relaxed, the recoil of the arterial walls, acting upon the column of blood, immediately closes the semilunar valves upon the two sides. The auricles continue to dilate, and the ventricles are slowly receiving blood. Immediately following the second sound, during the first part of the interval, the auricles become fully dilated; and, in the last part of the interval, immediately preceding the first sound, the auricles contract and the ventricles are fully dilated. This completes a single revolution of the heart.

Frequency of the Heart's Action.—Physicians have always attached the greatest importance to the frequency of the action of the heart, as one of the important indications of the general condition of the system. The variations which are met with in health, depending upon age, sex, muscular activity, the condition of the digestive system, etc., point to the fact that the action of the heart is closely allied to the various functions of the economy and readily sympathizes with their derangements. As each ventricular systole is followed by an expansion of the arteries, which is readily appreciated by the touch, it is more convenient to study the succession of these movements by exploring the vessels than by examination of the heart itself. Leaving out certain of the qualities of the pulse, this becomes an exact criterion of the acts of the heart.

The number of pulsations of the heart is not far from seventy per minute in an adult male and is from six to ten more in a female. There are individual cases, however, in which the pulse is normally much slower or more frequent than this, a fact which must be remembered when examining the pulse in disease. It is said that the pulse of Napoleon I. was only forty per minute. Dr. Dunglison mentions a case which came under his own observation, in which the pulse presented an average of thirty-six per minute. The same author states that the pulse of Sir William Congreve was never below one hundred and twenty-eight per minute, in health. It is by no means unfrequent to find a healthy pulse of a hundred or more a minute; but, in the cases reported in which the pulse has been found to be forty or less, it is possible that every alternate beat of the heart was so feeble as to produce no perceptible arterial pulsation. In this case, the fact may be ascertained by listening to the heart while the finger is placed upon the artery. Such an instance has lately come under our observation, in which the pulse was apparently but thirty-five per minute.

Influence of Age and Sex.—In both the male and female, observers have constantly found a great difference in the rapidity of the heart's action at different periods of life. The observations of Dr. Guy on this point are very numerous and were made with the utmost care with regard to the conditions of the system at the time the pulse was taken in each case. All were taken at the same hour and with the subject in a sitting posture. Dr. Guy found the pulsations of the heart in the fœtus to be pretty uniformly 140 per minute. At birth, the pulse is 136. It gradually diminishes during the first year to about 128. The second year, the diminution is quite rapid, the tables of Dr. Guy giving 107 as the mean frequency at two years of age. After the second year, the frequency progressively diminishes until adult life, when it is at its minimum, which is about 70 per minute. It is a common but erroneous impression that the pulse diminishes in frequency in old age. On the contrary, numerous observations show that at the later periods of life the movements of the heart become slightly accelerated, ranging from 75 to 80.

During early life there is no marked and constant difference in the rapidity of the pulse in the sexes; but, toward the age of puberty, the development of the sexual peculiarities is accompanied with an acceleration of the heart's action in the female, which continues even into old age. The differences at different ages are shown in the following table, compiled from the observations of Dr. Guy:

Ages.	Males. Average pulsations.	Females. Average pulsations.
From 2 to 7 years	97	98
" 8 " 14 "	84	94
" 14 " 21 "	76	82
" 21 " 28 "	73	80
" 28 " 35 "	70	78
" 35 " 42 "	68	78
" 42 " 49 "	70	77
" 49 " 56 "	67	76
" 56 " 63 "	68	77
" 63 " 70 "	70	78
" 70 " 77 "	67	81
" 77 " 84 "	71	82

Influence of Digestion.—The condition of the digestive system has a marked influence on the rapidity of the pulse, and there is generally an increase in the pulse of from five to ten beats per minute after each meal. Prolonged fasting diminishes its frequency by from twelve to fourteen beats. Alcohol first diminishes and afterward accelerates the pulse. Coffee is said to accelerate the pulse in a marked degree. It has been ascertained that the pulse is accelerated to a greater degree by animal than by vegetable food. These variations have long been recognized by physiologists.

Influence of Posture and Muscular Exertion.—It has been observed that the position of the body has a very marked influence upon the rapidity of the pulse. Experiments of a very interesting character have been made by Dr. Guy and others, with a view to determine the difference in the pulse in different postures. In the male, there is a difference of about ten beats between standing and sitting, and fifteen beats between standing and the recumbent posture. In the female, the variations with position are not so great. The average given by Dr. Guy is, for the male standing, 81; sitting, 71; lying, 66;—for the female: standing, 91; sitting, 84; lying, 80. This is given as the average of a large number of observations. There were a few instances, however, in which there was scarcely any variation with posture, and some in which the variation was much greater than the average. In the inverted posture, the pulse was found to be reduced about fifteen beats.

The question at once suggests itself whether the acceleration of the pulse in sitting and standing may not be due, in some measure, to the muscular effort required in making the change of posture. This is answered by the farther experiments of Dr. Guy, in which the subjects were placed on a revolving board, and the posture changed without any muscular effort. The same results as those cited above were obtained in these experiments, showing that the difference is due to the position of the body alone. In a single observation, Dr. Guy found the pulse, standing, to be 89; lying, 77; difference, 12. With the posture changed without any muscular effort, the results were as follows: standing, 87; lying, 74; difference, 13. Various theoretical explanations of these variations have been offered by physiologists; but Dr. Guy seems to have settled experimentally the fact that the acceleration is due in part to the muscular effort required to maintain the body in the sitting and standing positions. The following are the results of experiments which bear conclusively on this point, in which it is shown that when the body is carefully supported in the erect or sitting posture, so as to be maintained without muscular effort, the pulse is less frequent than when the subject is standing; and, furthermore, that the pulse is accelerated, in the recumbent posture, when the body is only partially supported:

"1. Difference between the pulse in the erect posture, without support, and leaning in the same posture, in an average of twelve experiments on the writer, 12 beats; and on an average of eight experiments on other healthy males, 8 beats.

"2. Difference in the frequency of the pulse in the recumbent posture, the body fully supported, and partially supported, 14 beats, on an average of five experiments.

"3. Sitting posture (mean of ten experiments on the writer), back supported, 80; unsupported, 87; difference, 7 beats.

"4. Sitting posture with the legs raised at right angles with the body (average of twenty experiments on the writer), back unsupported, 86; supported, 68; difference, 18 beats. An average of fifteen experiments of the same kind on other healthy males gave the following numbers: back unsupported, 80; supported, 68; a difference of 12 beats."

Influence of Exercise, etc.—It is a fact generally admitted that muscular exertion increases the frequency of the pulsations of the heart; and the experiments just cited show that the difference in rapidity, which is by some attributed to change in posture (some positions, it is fancied, offering fewer obstacles to the current of blood than others), is mainly due to muscular exertion. Every one knows, indeed, that the action of the heart is much more rapid after violent exertion, such as running, lifting, etc. Experiments on this point date from quite a remote period. Bryan Robinson, who published a treatise on the "Animal Economy" in 1734, states, as the result of observation, that a man in the recumbent position has 64 pulsations per minute; sitting, 68; after a slow walk, 78; after walking four miles in an hour, 100; and 140 to 150 after running as fast as he could. This general statement, which has been repeatedly verified, shows the powerful influence of the muscular system on the heart. The fact is so familiar that it need not be farther dwelt upon.

The influence of sleep upon the action of the heart reduces itself almost entirely to the proposition that, during this condition, we have an entire absence of muscular effort, and consequently the number of beats is less than when the individual is aroused. It has been found that there is no difference in the pulse between sleep and perfect quiet in the recumbent posture. This fact obtains in the adult male; but it is said by Quetelet that there is a marked difference in females and young children, the pulse being always slower during sleep.

Influence of Temperature.—The influence of extremes of temperature upon the heart is very decided. The pulse may be doubled by remaining a very few minutes exposed to extreme heat. Bence Jones and Dickinson have ascertained that the pulse may be very much reduced in frequency, for a short time, by the cold douche. It has also been remarked that the pulse is habitually more rapid in warm than in cold climates.

Although many circumstances materially affect the rapidity of the heart's action, they do not complicate, to any great extent, our examinations of the pulse in disease. In cases which present considerable febrile movement, the patient is generally in the recumbent posture. The variations induced by violent exercise are easily recognized, while those dependent upon temperature, the condition of the digestive system, etc., are so slight that they may practically be disregarded. It is necessary to bear in mind, however, the variations which exist in the sexes and at different periods of life, as well as the possibility of individual peculiarities, when the action of the heart may be extraordinarily rapid or slow.

Influence of Respiration upon the Action of the Heart.—The relations between the functions of circulation and respiration are very intimate, and one function cannot go on without the other. If circulation be arrested, the muscles, being no longer supplied with fresh blood, soon lose their contractile power, and respiration ceases. We shall also find that circulation is impossible if respiration be permanently arrested. When respiration is imperfectly performed, the action of the heart is slow and labored. All physicians are familiar with the slow, full pulse, indicating labored action of the heart, which occurs in profound coma. The effects of arrest of respiration are marked in all parts of the circulatory system, arteries, capillaries, and veins; but the disturbances thus produced all react upon the heart, and the modifications which take place in the action of this organ are of the greatest interest and importance.

If the heart be exposed in a living animal and artificial respiration be kept up, although the pulsations are increased in frequency and diminished in force, after a time they become perfectly regular and continue thus so long as air is adequately supplied to the lungs. Under these circumstances, we have the respiration entirely at our command and can study the effects of its arrest upon the heart with the greatest facility. If we arrest respiration, we observe the following changes in the action of the heart: For a few seconds pulsations go on as usual, but in about a minute they begin to diminish in frequency. At the same time, the heart becomes engorged with blood, and the distention of its cavities rapidly increases. For a time its contractions are competent to discharge the entire contents of the left ventricle into the arterial system, and a cardiometer applied to an artery will indicate a great increase in the pressure of blood. A corresponding increase in the movements of the mercury will be noted at each action of the heart, indicating that the organ is acting with abnormal vigor. If respiration be still discontinued, the engorgement becomes intense, the heart at each diastole being distended to its utmost capacity. It now becomes incapable of emptying itself, the contractions become very unfrequent, perhaps three or four in a minute, and are progressively enfeebled. The organ is dark, almost black, owing to the circulation of venous blood in its substance. If respiration be not resumed, this distention continues, the contractions become less frequent and more feeble, and in a few minutes they entirely cease.

The arrest of the action of the heart, under these circumstances, is chiefly mechanical. The unaërated blood passes with difficulty through the capillaries of the system, and, as the heart is constantly at work, the arteries become immensely distended. This is proven by the great increase in the arterial pressure while these vessels are full of black blood. If we now closely examine the heart and great vessels, we are able to note distinctly the order in which they become distended. These phenomena were particularly noticed and described by Prof. Dalton, and they demonstrate conclusively that, in asphyxia, the obstruction to the circulation commences, not in the lungs, as is commonly supposed, but in the capillaries of the system, and is propagated backward to the heart through the arteries. The distention of the heart in asphyxia is therefore due to the fact that unaërated blood cannot circulate in the systemic capillaries. When thus distended, the muscular fibres of the heart become paralyzed, like any muscle after a severe strain.

If respiration be resumed at any time before the heart's action has entirely ceased, the organ in a few moments resumes its normal function. We first notice a change from the dusky hue it has assumed to a vivid red, which is owing to the circulation of arterial blood in its capillaries. The distention then becomes gradually relieved, and, for a few moments, the pulsations are abnormally frequent. If we now open an artery, it will be found to contain red blood. An instrument applied to an artery will show a diminution in arterial pressure and in the force of the heart's action, if the arrest of respiration have been carried only far enough to moderately distend the heart; or there is an increase in the pressure and force of the heart, if its action have been nearly arrested. A few moments of regular insufflation will cause the pulsations to resume their normal character and frequency.

In the human subject, the effects of temporary or permanent arrest of respiration on the heart are undoubtedly the same as those observed in experiments upon the warm-blooded animals. In the same way, also, it is possible to restore the normal action of the organ, if respiration be not too long suspended, by the regular introduction of fresh air into the lungs. The numerous examples of animation restored by artificial respiration, in drowning, etc., are evidence of this fact. In cases of asphyxia, those measures by which artificial respiration is most effectually maintained have been found most efficient.

Certain individuals have been said to have the power of temporarily arresting the action of the heart by a voluntary suspension of respiration. The most remarkable case of this kind on record is that of Colonel Townshend, which is quoted in many works on physiology. Colonel Townshend was said to be able to arrest respiration and the action of the heart so completely as to simulate death. When in this condition, the pulse was not perceptible at the wrist or over the præcordia, a mirror held before the mouth was not tarnished, and he was to all appearances dead. On one occasion, in the presence of several medical gentlemen, he remained in this condition for half an hour; afterward the functions of respiration and circulation becoming gradually reëstablished. This, to say the least, is a very remarkable case, but it is credited by many physiologists.

Cause of the Rhythmical Contractions of the Heart.

The phenomena attending the action of the heart present few difficulties in their investigation, compared with the study of the cause of the regular contractions and relaxations, which commence early in fœtal development to terminate only with life. This interesting question has long engaged the attention of physiologists and has been the subject of numerous experiments and speculations. It would be idle to follow the various theories which have been proposed to account for this constant action, except as a subject of purely historical interest; for many of them are based upon a very imperfect knowledge of the phenomena of the circulation. At the present day, although we are perhaps as far as ever from a knowledge of the actual cause of the regular movements, we are pretty well acquainted with the various conditions by which they are regulated and modified. We know, for example, how to induce contraction in a living muscle or one which is just separated from the organism and has not yet lost what we call its vital properties, but we must confess our utter ignorance when we ask ourselves why it acts in response to a stimulus. The advances that have been made in chemistry and microscopical anatomy do not disclose the so-called vital principle; and when we come to examine the various conditions under which the heart will continue its contractions, we are arrested by the impossibility of fathoming the mystery of the cause of contraction. The heart is, anatomically, very much like the voluntary muscles; but it has a constant function to perform and seems to act without any palpable excitation, while the latter, which have an occasional function, act only under the influence of a natural stimulus, like the nervous force, or under artificial irritation. The movements of the heart are not the only examples of what seems to be spontaneous action. The ciliated epithelium is in motion from the beginning to the end of life, and will continue for a certain time, even after the cells are detached from the organism. This motion cannot be explained, unless we call it an explanation to say that it is dependent on vital properties. But if we are yet ignorant of the actual cause of the rhythmical contraction of the heart, we are pretty well acquainted with the influences which render its action regular, powerful, and sufficient for the purposes of the economy. It will facilitate our comprehension of this, to compare the action of the heart with that of the ordinary voluntary muscles.

In the first place, every one knows that the action of the heart is involuntary. We can neither arrest, retard, nor accelerate its pulsations by a direct effort of the will. In this statement, we of course except those examples of arrest by the stoppage of respiration or acceleration by violent exercise, etc. In this respect the heart differs from certain muscles, like the muscles of respiration, which act involuntarily, it is true, but the action of which may be temporarily arrested or accelerated by a direct voluntary effort. The last-mentioned fact gives us the difference between the heart and all other striated muscles. All of them, in order to contract, must receive a stimulus, either natural or artificial. The natural stimulus comes from the nervous centres and is conducted by the nerves. If the nerves going to any of the respiratory muscles, for example, be divided, the muscle is paralyzed and will not contract without some kind of irritation. Connection with the nervous system does not seem necessary to the action of the heart, for it will contract, especially in the cold-blooded animals, some time after its removal from the body.

When a muscle has been removed from the body and is subjected to a stimulus, such as galvanism or mechanical or chemical irritation, it is thrown into contraction; but, if carefully protected from irritation, it will remain quiescent. Contraction in this instance is evidently produced by the application of the stimulus; but the question arises, Why does the muscle thus respond to stimulation? This is a question which it is impossible to answer satisfactorily, but one concerning which our ideas, since the time of Haller, have assumed a definite form. This great physiologist called the property which causes the muscle thus to contract, irritability; which is nothing more nor less than an unexplained property inherent in the muscle and continuing so long as it retains its absolute physical and chemical integrity. More than a hundred years ago, Haller described certain tissues of the body as possessing this "irritability," such as the muscles, stomach, bladder, etc., and the different degrees of irritability with which each one was endowed. He applied this theory to the action of the heart, which he considered as the part endowed with irritability to the highest degree. His theory of the action of the heart was that its rhythmical contraction depended upon the irritability inherent in its muscular fibres. He was far from denying the various influences which modified this action, but regarded its actual power of contraction as independent.

Experiments have shown that the heart will pulsate for a time when removed from all connection with other parts of the organism.[1] In the cold-blooded animals, in which the irritability of the tissues remains for some time after death, this is particularly marked. It is not the blood in the cavities of the heart which causes it to contract, for it will pulsate when its cavities have been emptied. It is not the contact of the air, for the heart will pulsate in a vacuum. The heart does not receive its irritability from the nervous system, for, when removed from the body, it has no connection with the nervous system; and it is not probable that it receives any influence from sympathetic ganglia which have lately been discovered in its substance, for detached portions of the heart will pulsate, and the contractions of the organ will continue in animals poisoned with woorara, which is known to paralyze the motor system of nerves.[2]

[1] Numerous instances of contractions of the heart in cold-blooded animals continuing for a very long time after excision are on record. Dr. Dunglison, in his work on Physiology, mentions several instances in which the heart pulsated for from ten to twenty-four hours after removal from the body. The most remarkable examples of this prolonged action were in the heart of the sturgeon. In one instance, in an experiment on a large alligator, we found the heart pulsating, *in situ*, twenty-eight hours after the animal had been killed by the injection of a solution of woorara. The heart was then excised and continued to beat during a long series of experiments, until it was arrested by powerful compression with the hand after it had been filled with water and the vessels tied.

[2] It is stated by Friedländer that no portion of the heart, however small, will contract rhythmically unless it con-

It is unnecessary to refer to the various experiments which have demonstrated the independence of the contractions of the heart. They are of such a simple nature that they may be verified by any one who will take the trouble to excise the heart of a frog or turtle, place it under a small bell-glass so that it will not be subject to possible irritation from currents of air, and watch its pulsations. In such an observation as this, it is evident that, for a certain time, contractions, more or less regular, will take place; and the experiments referred to above show that they occur without any external influence. In short, it is evident that the muscular fibres of the heart possess an irritability, by virtue of which they will contract intermittently for a time, although no stimulus be applied; as the ordinary striated muscular fibres have an irritability, by virtue of which they will respond, for a time, to the application of a stimulus.

It is manifestly necessary that the action of the heart should be constant, regular, and powerful; and when we say that the irritability inherent in its muscular tissue is such that it will contract for a time without any external stimulus, we by no means assume that this is the cause of its physiological action. It is only an important and incontestable property of the muscular fibres of the heart, and its regular action is dependent upon other conditions.

In the first place, we have to inquire what makes the action of the heart regular. The answer to this is, that the changes of nutrition, by which, through the blood circulating in its substance, the waste of its tissue is constantly supplied, preserve the integrity of the fibres, and keep them, consequently, in a condition to contract. This is true, likewise, of the ordinary striated muscular fibres. If the supply of blood be cut off from the substance of the heart, especially in the warm-blooded animals, the organ soon loses its irritability. This was admirably shown by the experiments of Erichsen. This observer, after exposing the heart in a warm-blooded animal and keeping up artificial respiration, ligated the coronary arteries, thus cutting off the greatest part of the supply of blood to the muscular fibres. He found, as the mean of six experiments, that the heart ceased pulsating, although artificial respiration was continued, in 23½ minutes. After the pulsations had ceased, they could be restored by removing the ligatures and allowing the blood to circulate again in the substance of the heart.

In the second place, the regular and powerful contractions of the heart are provided for by the circulation of the blood through its cavities. Although the heart, removed from the body, will contract for a time without a stimulus, it can be made to contract during the intervals of repose by an irritant, such as the point of a needle or a feeble current of galvanism. For a certain time after the heart has ceased to contract spontaneously, contractions may be induced in this way. This can easily be demonstrated in the heart of any animal, warm-blooded or cold-blooded. This irritability, which is manifested, under these circumstances, in precisely the same way as in ordinary muscles, is different in degree in different parts of the organ. Haller and others have shown that it is greater in the cavities than on the surface; for, long after irritation applied to the exterior fails to excite contraction, the organ will respond to a stimulus applied to its interior. The experiments of Haller also show that fluids in the cavities of the heart have a remarkable influence in exciting and keeping up its contractions. This observation is of much interest, as showing conclusively that the presence of blood is necessary to the natural and regular action of the heart. We quote one of the experiments on this point performed upon a cat:

" . . . . The superior vena cava having been divided, and the inferior ligated, and the pulmonary artery opened, and the right ventricle emptied by a sufficient compression, and the aorta ligated, all with promptitude, I saw the right auricle repose first, the right ventricle continued to beat for some time in unison with the left ventri-

tain ganglia; but this point cannot be regarded as definitively settled and is exceedingly difficult to determine. The fact that nervous and muscular irritability are entirely distinct from each other is a strong argument in favor of the independent irritability of the muscular tissue of the heart.

cle, and its walls descended toward the middle line of the heart: but this ventricle did not delay to lose its movement the first. As for the other ventricle, which could no longer empty itself into the aorta, it was filled with blood and its movement continued for four hours. . . ."

This experiment was confirmed by numerous others. It will be observed that one side of the heart was made to cease its pulsations, while the other side continued to contract, by simply removing the blood from its interior; which conclusively proves that, although the heart may act for a time independently, the presence of blood in its cavities is a stimulus capable of prolonging its regular pulsations. Schiff has gone still farther, and has succeeded in restoring the pulsations in the heart of a frog, which had ceased after it had been emptied, by introducing a few drops of blood into the auricle. Our own experiments upon the hearts of alligators and turtles show that, when removed from the body and emptied of blood, the pulsations are feeble, rapid, and irregular; but that when filled with blood, the valves being destroyed so as to allow free passage in both directions between the auricles and ventricle, the contractions become powerful and regular. In these experiments, when water was introduced instead of blood, the pulsations became more regular, but were more frequent and not so powerful as when blood was used. These experiments show also that the action of the heart may be affected by the character, particularly the density, of the fluid which passes through it, which may explain its rapid and feeble action in anæmia.

It seems well established that the heart, although capable of independent action, is excited to contraction by the blood as it passes through its cavities. A glance at the succession of its movements, particularly in cold-blooded animals, in which they are so slow that the phenomena can be easily observed, will show how these contractions are induced. If we look at the organ as it is in action, we see first a distention of the auricle, and this is immediately followed by a contraction filling the ventricle, which in its turn contracts. Undoubtedly, the tension of the fibres, as well as the contact of blood in its interior, acts as a stimulus; and, as all the fibres of each cavity are put on the stretch at the same instant, they contract simultaneously. The necessary, regular distention of each cavity thus produces rhythmical and forcible contractions; and the mere fact that the action of the heart alternately empties and dilates its cavities insures regular pulsations, so long as blood is supplied and no disturbing influences are in operation.

The muscular fibres of the heart seem to be endowed with an inherent property, called irritability, by virtue of which they will contract for a certain time without the application of a stimulus. Irritability, manifested in this way, continues so long as, by the processes of nutrition, the fibres are maintained in their integrity. The muscular tissue, however, may be thrown into contraction, during the intervals of repose, by the application of a stimulus, a property which is observed in all muscular fibres. The irritability manifested in this way is much more marked in the interior than on the exterior of the organ. Blood in contact with the lining membrane of the heart acts as a stimulus in a remarkable degree and is even capable of restoring irritability after it has become extinct. The passage of blood through the heart is the natural stimulus of the organ and may be said to be the cause of its regular pulsations, although it by no means endows the fibres with their contractile properties.

Influence of the Nervous System on the Heart.

The movements of the heart, as we have seen, are not directly under the control of the will; and observations on the human subject, as well as on living animals, have shown that the organ is devoid of general sensibility. The latter fact was demonstrated in the most satisfactory manner by Harvey, in the case of the Viscount Montgomery. In this case, the heart was exposed, and Harvey found that it could be touched and handled without even the knowledge of the subject. This has been verified in other instances in the human subject. Its physiological movements are capable of being influenced in a remarkable degree through the nervous system, notwithstanding this insensibility and in spite of the fact that the muscular fibres composing it are capable of contraction when removed from all connection with the body and that the regular pulsations can be kept up for a long time by the mere passage of blood through its cavities. The influence thus exerted is so great, that some eminent authorities have held the opinion that the cause of the irritability of the organ was derived from the nerves. One of the most distinguished advocates of this opinion was Legallois. This observer arrested the action of the heart of the rabbit by suddenly destroying the spinal cord, from which he drew the conclusion that the heart derived its contractile power from the cerebro-spinal system. The experiments which we have already cited, showing the continuance of the heart's action after excision, disprove this so completely, that it was not thought worth while to discuss this view while treating of the cause of its rhythmical contractions. The same may be said with regard to the experiments of Brachet, in which he endeavored to prove that the contractility of the heart is derived from the cardiac plexus of the sympathetic system of nerves. The fact that the heart does not depend for its contractility upon external nervous influence may be regarded as long since definitely settled; but within a few years the discovery in its substance of ganglia belonging to the sympathetic system has revived, to some extent, the view that its irritability is derived from nerves. It is not necessary to follow out all the experiments which combine to demonstrate the incorrectness of this view. Bernard, by a series of admirably-conceived experiments upon the effects of the woorara poison, has succeeded in demonstrating the distinction between muscular and nervous irritability. In an animal killed with this remarkable poison, the functions of the motor nerves are entirely abolished, so that galvanization or other irritation does not produce the slightest effect; yet the muscles retain their irritability, and, if artificial respiration be kept up, the circulation will continue for a long time. The heart, by this means, seems to be isolated from the nervous system as completely as if it were excised; and galvanization of the pneumogastric nerves in the neck, which, in a living animal, will immediately arrest its action, has no effect. On the other hand, poisoning by the sulphocyanide of potassium destroys the muscular irritability and leaves the nerves intact. By these experiments, which we have frequently repeated, we can completely separate the nervous from the muscular irritability and show their entire independence of each other; and there is every reason to suppose that the heart, like the other muscles, does not derive its contractility from any other system. It is evident, however, that the heart is often powerfully influenced through the nerves. Sudden and violent emotions will occasionally arrest its action and have been known to produce death. Palpitations are to be accounted for in the same way. Some of the modifications which we have already considered, depending on exercise, digestion, etc., are effected through the nerves; and it is through this system that the heart and all the important organs of the body are made to a certain extent mutually dependent. It becomes interesting and highly important, then, to study their influences and follow out, as clearly as possible, the action of the nerves which are distributed to the heart.

The anatomical connections of the heart with the nervous centres are mainly through the sympathetic and the pneumogastric nerves. We can study the influence of these nerves to most advantage in two ways; first, by dividing them and watching the effect of depriving the heart of their influence, and second, by exciting them by means of a feeble current of galvanism. It is well known that in an animal just killed the "nervous force" may be closely imitated by galvanism, which is better than any other means of stimulation, as it does not affect the integrity of the nerves and the amount of the irritation may be easily regulated.[1]

[1] We shall not discuss the effects upon the heart of sudden destruction of the great nervous centres. It has been shown that the heart becomes arrested when the brain is crushed, as by a blow with a hammer, when the medulla

Experiments on the influence of the sympathetic nerves upon the heart are not quite so satisfactory as we might desire. It has been asserted that the action of the heart is immediately arrested by destroying the cardiac plexus. With regard to this, we must take into account the difficulty of making the operation and the disturbance of the heart consequent upon the necessary manipulations. It has been shown pretty conclusively, however, that stimulation of the sympathetic in the neck has the effect of accelerating the pulsations of the heart. The extreme difficulty of dividing all the branches of the sympathetic going to the organ leaves a doubt as to whether such an operation would definitely abridge its action.

We have next to consider the influence of the pneumogastrics upon the heart. Experiments on these nerves are made with greater facility than on the nerves of the sympathetic system, and the results are much more satisfactory. Like all the cerebro-spinal nerves, the influence generated in the nervous centre from which they take their origin is conducted along the nerve and manifested at its distribution. When they are divided, we may be sure that, as far as they are concerned, all the organs which they supply are cut off from nervous influence; and, when galvanized in their course, we imitate or exaggerate the influence sent from the nervous centre.

The invariable effect on the heart of division of the pneumogastric nerves in the neck is an increase in the frequency and a diminution in the force of its pulsations. One or two writers have denied this fact, but it is confirmed by the testimony of nearly all experimenters. To anticipate a little in the history of the pneumogastric nerves, it may be stated that, while they are exclusively sensitive at their origin, they receive, after having emerged from the cranial cavity, a number of filaments from various motor nerves. That they influence certain muscles, is shown by the paralysis of these muscles after division of the nerves in the neck, as, for example, the arrest of the movements of the glottis. Having this double property of motion and sensation, and being distributed in part to an organ composed almost exclusively of muscular fibres, which, as we have seen, is not endowed with general sensibility, we should expect that their section would arrest, or at least diminish, the frequency of the heart's action. What explanation, then, can we offer for the fact that this seems actually to excite the movements of the heart? We shall be better prepared to answer this question after we have studied the effects of galvanization of the nerves in a living animal or in one in which the action of the heart is kept up by artificial respiration.

Numerous experiments have been made with reference to the effects on the heart of galvanic currents, both feeble and powerful, passed through the pneumogastrics before division, of currents passed through the upper and lower extremities after division, etc., a full detail of which belongs properly to the physiological history of the nervous system. In this connection, a few of these facts only need be stated.

It has been shown by repeated experiments, which we have frequently confirmed, that a moderately-powerful interrupted galvanic current passed through both pneumogastrics will arrest the action of the heart, and that the organ remains quiescent so long as the current is continued. This experiment has been performed upon living animals, both with and without exposure of the heart. The arrest is not due to violent and continued contraction of the muscular fibres; on the contrary, the heart is relaxed, its ventricles are flaccid, and its fibres are for the time paralyzed. The question then arises whether this action be exerted directly on the heart through the nerves, or whether an influence be conveyed to the nervous centre and transmitted to the heart in another way. This is settled by the experiment of dividing the nerves and galvanizing alternately the extremities connected with the heart and those connected with the nervous centres. It has

oblongata or the spinal cord is suddenly destroyed, and even the crushing of a foot, in the frog, has been known to product this effect. In fine, this may be done by any extensive injury to the nervous system; but this fact does not teach us much with regard to the physiological influences of the nerves. For example, while crushing of the brain arrests the heart, the brain may be removed from a living animal and the heart will beat for days. Experiments upon the influence of the medulla oblongata and spinal cord are by no means satisfactory.

been ascertained that galvanization of the extremities connected with the heart arrests its action, while galvanization of the central extremities has no such effect. Another interesting fact also shows that the influence exerted upon the heart is through the motor filaments of the pneumogastrics. It has been demonstrated by Bernard, in a very curious series of experiments which we shall not fully discuss in this connection, that the woorara poison paralyzes only the motor nerves, leaving the sensory nerves intact. If we expose the heart and the pneumogastric nerves in a warm-blooded animal poisoned with this agent, and continue the pulsations by keeping up artificial respiration, we find that the most powerful current of galvanism passed through the pneumogastrics has no effect upon the heart.

When we come to the study of the nervous system, we shall see that the inhibitory action of the pneumogastrics upon the heart is derived from the spinal accessory nerves, a fact which has been proven beyond question by a very ingenious series of experiments, which will be fully described hereafter.

Although galvanization of the pneumogastrics arrests the action of the heart in nearly all animals, there are some in which this does not take place, as in birds; a fact which is stated by Bernard, but for which he offers no explanation. In some experiments instituted on this subject a few years ago on alligators, we noticed a singular peculiarity which throws some light on the question we are now considering. Desiring to demonstrate to the class at the New Orleans School of Medicine the action of the heart in this animal, an alligator six feet in length was poisoned with woorara and the heart exposed. The animal came under the influence of the poison in about thirty minutes, when the dissection was commenced, and was quite dead when the heart was exposed. The pneumogastrics were then exposed and galvanized, with the effect of promptly arresting the action of the heart. This observation was verified in another experiment. We were at first at a loss to account for the absence of effect of the woorara on the motor filaments of the pneumogastric nerves; but on reflection we thought it might be due to slow absorption of the poison in so large a cold-blooded animal. With a view of ascertaining whether there be any difference in the promptness with which different nerves in the body are affected by this agent, we made the following experiment upon a dog: The animal was brought under the influence of ether, and the heart, the pneumogastrics, and the sciatic nerve were exposed. Galvanization of the sciatic produced muscular contraction, and stimulation of the pneumogastrics arrested the heart promptly. A grain of woorara, dissolved in water, was then injected under the skin of the thigh. One hour after the injection of the woorara, the sciatic was found insensible to galvanism, but the heart could be arrested by galvanization of the pneumogastrics, although it required a powerful current. A weaker current diminished the frequency and increased the force of its pulsations. In this experiment, the operation of opening the chest undoubtedly diminished the activity of absorption of the poison and consequently retarded its effects upon the nervous system. Taken in connection with the observations on alligators, it shows that the motor nerves are not all affected at the same time, and that the pneumogastrics resist the action of this peculiar poison after the motor nerves generally are paralyzed.

Our knowledge of the inherent properties of the muscular fibres of the heart and of the effects of the passage of blood through its cavities, which together are competent to keep up for a time regular pulsations without the intervention of the nervous system, taken in connection with the facts just stated concerning the influence of section or galvanization of the pneumogastric nerves, enables us to comprehend pretty well the influence of these nerves on the heart. They undoubtedly perform the important function of regulating the force and frequency of its pulsations. Hardly any reflection is necessary to convince us of the importance of such a function, and how it must of necessity be accomplished through the pneumogastrics. It is important, of course, that the heart should act at all times with nearly the same force and frequency. We have seen that the inherent properties of its fibres are competent to make it contract, and the necessary intermittent dilatation of its cavities makes these contractions assume a certain regularity; but the quantity and density of the blood are subject to very considerable variations within the limits of health, which, without some regulating influence, would undoubtedly cause variations in the heart's action, so considerable as to be injurious. This is shown by the comparatively-inefficient and palpitating action of the heart when the pneumogastrics are divided. These nerves convey to the heart a constant influence, which we may compare to the insensible tonicity imparted to voluntary muscles by the general motor system. For we know that when a set of muscles on one side is paralyzed, as in facial palsy, their tonicity is lost, they become flaccid, and the muscles on the other side, without any effort of the will, distort the features. We can imitate an exaggeration of this force by a feeble current of galvanism, which renders the pulsations of the heart less frequent and more powerful, or exaggerate it still more by a more powerful current, which arrests the action of the heart altogether. Phenomena are not wanting in the human subject to verify these views. Causes which operate through the nervous system frequently produce palpitation and irregular action of the heart. Cases are not uncommon in which palpitation habitually occurs after a full meal. There are instances on record of immediate death from arrest of the heart's action as a consequence of fright, anger, grief, or other severe mental emotions. Syncope from these causes is by no means uncommon. In the latter instance, when the heart resumes its functions, the nervous shock carried along the pneumogastrics is only sufficient to arrest its action temporarily. When death takes place, the shock is so great that the heart never recovers from its effects.

Summary of certain Causes of Arrest of the Action of the Heart.

In warm-blooded animals, the heart's action speedily ceases after it is deprived of its natural stimulus, the blood. It is not from experiments on the inferior animals alone that we derive proof of this fact. It is well known that, in profuse hæmorrhage in the human subject, the contractions of the heart are progressively enfeebled, and, when the loss of blood has proceeded to a certain extent, are permanently arrested. Cases of transfusion after hæmorrhage show that when blood is introduced the heart may be made to resume its pulsations. The same result takes place in death by asthenia; and cases are on record in which life has been prolonged, as in hæmorrhage, by transfusion of even a small quantity of healthy blood. These facts have been demonstrated on the inferior animals by experiments already cited. The experiment of Haller, in which the action of the right side of the heart of a cat was arrested by emptying it of blood, while the left side, which was filled with blood, continued to pulsate, showed that the absence of blood in its cavities is competent of itself to arrest the heart. The experiments of Erichsen, who paralyzed the heart by ligating the coronary arteries, and of Schiff, who produced a local paralysis by ligating the vessel going to the right ventricle, show that the heart may also be arrested by cutting off the circulation of blood in its substance. Both of these causes must operate in arrest of the heart's action in hæmorrhage.

The mechanical causes of arrest of the heart's action are of considerable pathological importance. The heart, in common with other muscles, may be paralyzed by mechanical injury. A violent blow upon the deltoid paralyzes the arm; a severe strain will paralyze the muscles of an extremity; and, in the same way, excessive distention of the cavities of the heart will arrest its pulsations. This is shown by arrest of the circulation in asphyxia. We have already seen that, under these circumstances, the heart is incapable of forcing the unaërated blood through the systemic capillaries. The heart finally becomes enormously strained and distended and is consequently paralyzed. The same result follows the application of a ligature to the aorta. This effect may be produced, also, in the cold-blooded animals, in which, if the heart be left undisturbed, the pulsations will continue for a long time. The following experiment illustrating this point was performed upon the heart of an alligator six feet in length:

The animal was poisoned with woorara, and twenty-eight hours after death the heart, which had been exposed and left *in situ*, was pulsating regularly. It was then removed from the body, and, after some experiments on the comparative force, etc., of the pulsations when empty and when filled with blood, was filled with water, the valves having been destroyed so as to allow free passage of the fluid through the cavities, and the vessels ligated. The ventricles, still filled with water confined in their cavity, were then firmly compressed with the hand, so as to subject the muscular fibres to powerful compression. From that time, the heart entirely ceased its contractions and became hard like a muscle in a state of cadaveric rigidity. This experiment shows how completely and promptly the heart, even of a cold-blooded animal, may be arrested in its action by mechanical injury.

Cases of death from distention of the heart are not infrequent in practice. It is well established that the form of organic disease which most frequently leads to sudden death is that in which the heart is liable to great distention. We refer to disease at the aortic orifice. In other lesions there is not this tendency; but, when the aortic orifice is contracted or the valves are insufficient, any great disturbance of the circulation will cause the heart to become engorged, which is liable to produce a fatal result.

Most persons are practically familiar with the distressing sense of suffocation which frequently follows a blow upon the epigastrium; and a few cases are on record of instantaneous death following a comparatively slight concussion in this region. We had an opportunity, in the winter of 1854–'5, of witnessing an autopsy in a case of this kind. A young mulatto man, employed as a waiter at the Louisville Hotel, received a blow in the epigastrium while frolicking, which produced instantaneous death. On post-mortem examination, no lesion was discovered. Although these cases are rare, they are well recognized, and the effects are generally attributed to injury of the solar plexus. The distress is precisely what would occur from sudden arrest of the heart's action; for it is the blood charged with oxygen and sent by the heart to the system, which supplies the wants of the tissues, and not the simple entrance of air into the lungs; and arrest of the circulation of arterial blood, from any cause, produces suffocation as completely as though the trachea were ligated. This fact we have clearly proven by experiments. It is a question whether the arrest of the heart, if this be the pathological condition, be due to concussion of the nervous centre or to the direct effects of the blow upon the organ itself. Our present data do not enable us to answer this question definitely, but they rather incline us to the opinion that in such accidents the symptoms are due to direct injury of the heart. An additional argument in favor of this view is founded on our knowledge of the mode of operation of the sympathetic system. The effects of stimulation or irritation of this system are not instantaneously manifested, as is the case in the cerebro-spinal system, but are developed slowly and gradually.

As far as we have been able to learn by experiment, the nervous influences which arrest the action of the heart operate through the pneumogastrics and are derived from the spinal accessory nerves. As we have just seen, we can closely imitate this action by galvanism. The causes of arrest in this way are numerous. Among them may be mentioned, sudden and severe bodily pain and severe mental emotions. With the exception of arrest of the heart from loss of blood and from distention, from whatever cause it may occur, stoppage of the heart takes place from influences operating through the nervous system. It may be temporary, as in syncope, or it may be permanent; and examples of the latter, though rare, are sufficiently well authenticated.

CHAPTER III.

CIRCULATION OF THE BLOOD IN THE VESSELS.

Physiological anatomy of the arteries—Course of blood in the arteries—Locomotion of the arteries and production of the pulse—Pressure of blood in the arteries—Pressure in different parts of the arterial system—Depressor nerve—Influence of respiration on the arterial pressure—Rapidity of the current of blood in the arteries—Rapidity in different parts of the arterial system—Circulation of the blood in the capillaries—Physiological anatomy of the capillaries—Capacity of the capillary system—Course of blood in the capillaries—Relations of the capillary circulation to respiration—Causes of the capillary circulation—Influence of temperature on the capillary circulation—Influence of direct irritation on the capillary circulation—Circulation of the blood in the veins—Physiological anatomy of the veins—Course of the blood in the veins—Pressure of blood in the veins—Rapidity of the venous circulation—Causes of the venous circulation—Air in the veins—Function of the valves—Conditions which impede the venous circulation—Regurgitant venous pulse—Circulation in the cranial cavity—Circulation in erectile tissues—Derivative circulation—Pulmonary circulation—Rapidity of the circulation—Phenomena in the circulatory system after death.

In man and in all animals possessed of a double heart, each contraction of this organ forces a charge of blood from the right ventricle into the pulmonary artery, and from the left ventricle into the aorta. We have seen how the valves which guard the orifices of these vessels effectually prevent regurgitation during the intervals of contraction. There is, therefore, but one direction in which the blood can flow in obedience to this intermittent force; and the fact that, even in the smallest arteries, there is an acceleration in the current coincident with each contraction of the heart, which disappears when the action of the heart is arrested, shows that the ventricular systole is the prime cause of the arterial circulation. But this part of the physiology of the circulation is not so simple as we might at first be led to suppose. The arteries have the important function of supplying nutritive matter to all the tissues, of furnishing to the glands materials out of which the secretions are formed, and, in short, are the vessels of supply to every part of the organism. The supply of blood regulates, to a considerable extent, the processes of nutrition and has an important bearing on the general and special functions; and the various physiological processes necessarily demand considerable modifications in the quantity of arterial blood which is furnished to parts at different times. For example, during secretion, the glands require several times as much blood as in the intervals of their action. The force of the heart, we have seen, varies but little within the limits of health; and the conditions necessary to the proper distribution of blood in the economy are regulated almost exclusively by the arterial system. These vessels are not inert tubes, but are endowed with elasticity, by which the circulation is considerably facilitated, and with contractility, by which the supply to any part may be modified, independently of the action of the heart. Sudden flushes or pallor of the countenance are examples of the facility with which this may be effected. It is evident, therefore, that the properties of the coats of the arteries are of great physiological importance. We shall then commence the study of this division of the circulatory system with a consideration of its physiological anatomy.

Physiological Anatomy of the Arteries.

The vessels which carry the venous blood to the lungs are branches of a great trunk which takes its origin from the right ventricle. They do not differ in structure from the vessels which carry the blood to the general system, except in the fact that their coats are somewhat thinner and more distensible. The aorta, branches and ramifications of which supply all parts of the body, is given off from the left ventricle. Just at its origin, behind the semilunar valves, the aorta has three sacculated pouches, called the sinuses of Valsalva. Beyond this point the vessels are cylindrical. As we recede from the heart, the arteries branch, divide, and subdivide, until they are reduced to microscopic size. The branches, with the exception of the intercostal arteries, which make nearly a right angle with the thoracic aorta, are given off at an acute angle. As a rule, the arteries are nearly straight, taking the shortest course to the parts which they supply with blood; and, while the branches progressively diminish in size, but few are given off between the great trunk and the small vessels which empty into the capillary system. Haller counted but twenty branches of the mesenteric artery between the aorta and the capillaries of the intestines. So long as a vessel gives off no branches, its caliber does not progressively diminish; as the common carotids, which are as large at their bifurcation as they are at their origin. There are one or two instances in which vessels, although giving off numerous branches in their course, do not diminish in size for some distance; as the aorta, which is as large at the point of division into the iliacs as it is in the chest, and the vertebral arteries, which do not diminish in caliber until they enter the foramen magnum. With these exceptions, as we recede from the heart, the caliber of the vessels progressively diminishes. It has long been remarked that the combined caliber of the branches of an arterial trunk is much greater than that of the main vessel; so that the arterial system, as it branches, increases in capacity.

The arrangement of the arteries is such that the requisite supply of blood is sent to all parts of the economy by the shortest course and with the least expenditure of force from the heart. Generally, the vessels are so situated as not to be exposed to pressure and consequent interruption of the current of blood; but, in certain situations, as about some of the joints, there is necessarily some liability to occasional compression. In certain situations, also, as in the vessels going to the brain, particularly in some of the inferior animals, it is necessary to moderate the force of the blood-current, on account of the delicate structure of the organs in which they are distributed. Here Nature makes a provision in the shape of anastomoses, by which, on the one hand, compression of a vessel simply diverts, and does not arrest the current of blood, and, on the other hand, the current is rendered more equable and the force of the heart is moderated.

The arteries are provided with membranous sheaths, of greater or less strength, as the vessels are situated in parts more or less exposed to disturbing influences or accidents.

Researches into the minute anatomy of the arteries have shown that they are possessed of three pretty well marked coats. As these vary very considerably in arteries of different sizes, it will be convenient, in their description, to divide the vessels into three classes:

1. *The largest arteries;* in which are included all that are larger than the carotids and common iliacs.

2. *The arteries of medium size;* that is, between the carotids and iliacs and the smallest.

3. *The smallest arteries;* or those less than $\frac{1}{12}$ or $\frac{1}{13}$ of an inch in diameter.

The largest arteries are endowed with great strength and elasticity. Their external coat is composed of white, or inelastic fibrous tissue, with a few longitudinal and oblique fasciculi of involuntary muscular fibres. This coat is no thicker in the largest vessels than in some of the vessels of medium size; and in some medium-sized vessels it is actually thicker than in the aorta. This is the only coat which is vascular.

The middle coat, on which the thickness of the walls of the vessel depends, is composed chiefly of the yellow elastic tissue. This tissue is disposed in numerous layers. First we have a thin layer of ramifying elastic fibres, and then a number of layers of elastic membrane, with numerous oval longitudinal openings, which has given it the name of the "fenestrated membrane." Between the different layers of this membrane are found a few unstriped or involuntary muscular fibres. These muscular fibres, however, are not numerous and have but little physiological importance. A small portion of the aorta and pulmonary artery next the heart is entirely free from muscular fibres. In the largest arteries, the fibres are arranged in fasciculi, with amorphous and fibrous connective tissue running in a circular, longitudinal, and oblique direction. The longitudinal and oblique fibres exist chiefly in the outer coat. The middle coat of the largest arteries gives them their yellowish hue and the elasticity for which they are so remarkable.

The internal coat of the largest arteries does not differ materially from the lining membrane of the rest of the arterial system. It is identical in structure with the endocardium, the membrane lining the cavities of the heart, and is continued through the entire vascular system. It is a thin, homogeneous, elastic membrane, covered with a layer of elongated epithelial scales, with oval nuclei, their long diameter following the direction of the vessel.

The arteries of medium size possess considerable strength, some elasticity, and very great contractility. In the outer and inner coats we do not distinguish any great difference between these and the largest arteries, even in thickness. The essential difference

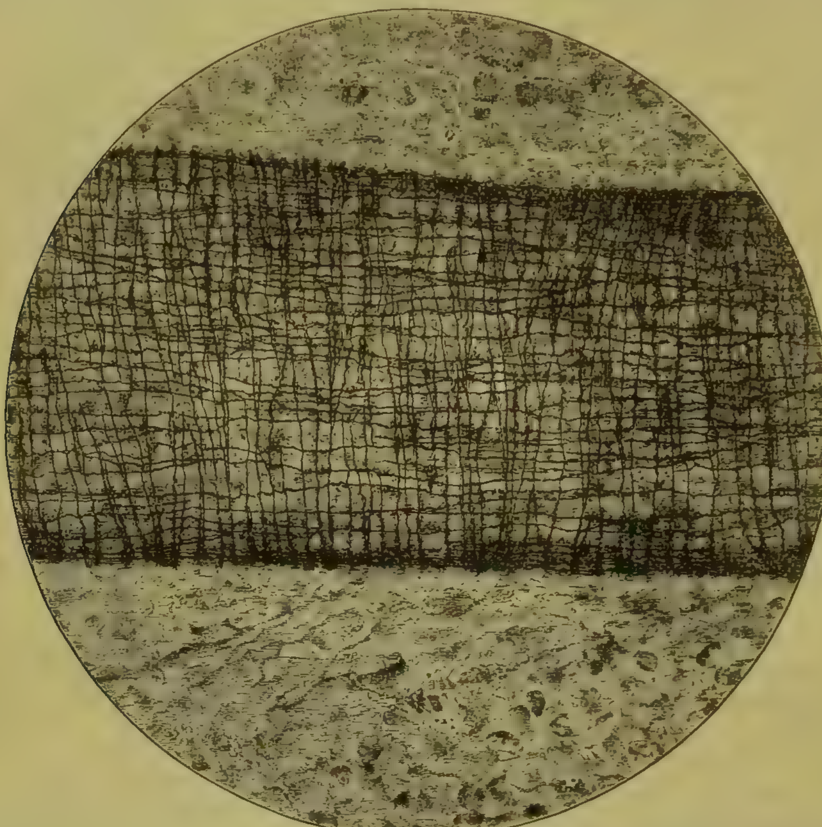


FIG. 20.—*Small artery from the mesentery of the frog, showing epithelium and circular muscular fibres; magnified 500 diameters.* (From a photograph taken at the United States Army Medical Museum.)

in the anatomy of these vessels is found in the middle coat. Here we have a continuation of the elastic elements found in the largest vessels, but relatively diminished in thickness and mingled with the fusiform, involuntary muscular fibres arranged, for the most part, at right angles to the course of the vessel. These fibres are found chiefly in the inner layers of the middle coat, and only in arteries smaller than the carotids and primitive iliacs. In arteries of medium size, like the femoral, profunda femoris, radial, or ulnar, they exist in several layers. There is no distinct division, as regards the middle coat, between the largest arteries and those of medium size. As we recede from the heart, muscular fibres gradually make their appearance between the elastic layers, progressively increasing in quantity, while the elastic elements are diminished.

In the smallest arteries, the external coat is thin and disappears just before the vessels empty into the capillary system; so that the very smallest arterioles have only the inner coat and a layer of muscular fibres. Although the greatest part of the muscular fibres in the middle coat of the arteries are arranged at right angles to the course of the vessels, nearly all of the arteries, in the human subject, are provided with longitudinal and oblique muscular fasciculi, which are sometimes external, sometimes internal, and sometimes on both sides of the circular layers.

The middle coat is composed of circular muscular fibres, without any admixture of elastic elements. In vessels $\frac{1}{100}$ of an inch in diameter, we have two or three layers of fibres; but, as we near the capillaries and as the vessels lose the external fibrous coat, these fibres exist in a single layer.

The internal coat presents no essential difference from the coat in other vessels, with the exception that the epithelium is less distinctly marked.

A tolerably-rich plexus of vessels is found in the external coats of the arteries. These are called the vasa vasorum and come from the adjacent arterioles, having no direct connection with the vessel on which they are distributed. A few vessels penetrate the external layers of the middle coat, but none are ever found in the internal coat.

Nervous filaments, principally from the sympathetic system, accompany the arteries, in all probability to their remotest ramifications. These are not distributed in the walls of the large vessels, but rather follow them in their course, their filaments of distribution being found in those vessels in which the muscular element of the middle coat predominates. When we come to treat of the physiology of the organic system of nerves, we shall see that the "vaso-motor" nerves play an important part in regulating the function of nutrition. Lymphatics have not been found in the coats of any of the blood-vessels.

Course of the Blood in the Arteries.—At every pulsation of the heart, all the blood contained in the ventricles, excepting, perhaps, a few drops, is forced into the great vessels. We have already studied the valvular arrangement by which the blood, once forced into these vessels, is prevented from returning into the ventricles during the diastole. The sketch we have given of the anatomy of the arteries has prepared us for a complexity of phenomena in the circulation in these vessels, which would not obtain if they were simple, inelastic tubes. In this case, the intermittent force of the heart would be felt equally in all the vessels, and the arterial circulation would be subject to no modifications which did not come from the action of the central organ. As it is, the blood is received from the heart into vessels endowed, not only with great elasticity, but with contractility. The elasticity, which is the prominent property of the largest arteries, moderates the intermittency of the heart's action, providing a continuous supply to the parts; while the contractility of the smallest arteries is capable of increasing or diminishing the supply in any part, as may be required in the various functions.

Elasticity of the Arteries.—This property, which is particularly marked in large vessels, has long been recognized. If, for example, we forcibly distend the aorta with water, it may be dilated to more than double its ordinary capacity and will resume its original size and form as soon as the pressure is removed. This simple experiment teaches us that, if the force of the heart be sufficient to distend the great vessels, their elasticity during the intervals of its action must be continually forcing the blood toward the periphery. The fact that the arteries are distended at each systole is abundantly proven by actual experiment; although the immense capacity of the arterial system, as compared with the small charge of blood which enters at each pulsation, renders the actual distention of the vessels less than we should be led to expect from the force of the heart's contraction. The most satisfactory experiments on this subject are those of Poiseuille. This observer illustrated the dilatation of the arteries in the following way: Having exposed a considerable extent of the primitive carotid in a horse, he enclosed a portion in a tin tube filled with water and connected with a small upright graduated tube of glass. The openings around the artery, as it passed in and out of the apparatus, being carefully sealed with tallow, it is evident that any dilatation of the vessel would be indicated by an elevation of the water in the graduated tube. This experiment invariably showed a marked dilatation of the artery with each contraction of the heart.

It being fully established that the arteries are dilated with each ventricular systole, it becomes important to study the influence of their elasticity upon the current of blood. Division of an artery in a living animal exhibits one of the important phenomena due to the elastic and yielding character of its walls. We observe, even in vessels of considerable size, as the carotid or femoral, that the flow of blood is not intermittent but remittent. With each ventricular systole, there is a sudden and marked impulse; but, during the intervals of contraction, the blood continues to flow with considerable force. As we recede from the heart, the impulse becomes less and less marked; but it is not entirely lost, even in the smallest vessels, the flow becoming constant only in the capillary system. That the force of the heart is absolutely intermittent, is shown by the following experiment: If the heart be exposed in a living animal, and a canula be introduced through the walls into one of the ventricles, we have a powerful jet at each systole, but no blood is discharged during the diastole. The same absolute intermittency of the current will be seen if the aorta be divided. It is evident that we must look to the arteries themselves for the force which produces a flow of blood during the intervals of the heart's action. The conversion of the intermittent current in the largest vessels into a nearly-constant flow in the smallest arterioles is effected by the physical property of elasticity. This may be illustrated in any elastic tube of sufficient length. If we connect with a syringe a series of rubber tubes progressively diminishing in caliber and discharging by a very small orifice, and inject water in an intermittent current, if the apparatus be properly adjusted, the fluid will be discharged at the end of the tube in a continuous stream. Nearer the syringe, the stream will be remittent; and, directly at the point of connection of the syringe with the tube, the stream will be intermittent. The intermittent impulse may be said, in this case, to be progressively absorbed by the elastic walls of the tube. Each impulse first distends that portion of the tube nearest to it, and farther on the distention is diminished until it becomes inappreciable. If the syringe be connected with two tubes, one elastic and the other inelastic, the current will be either remittent or continuous in the one, and intermittent in the other. This modification of the impulse of the heart has great physiological importance; for it is evidently essential that the current of blood, as it flows into the delicate capillary vessels, should not be alternately intermitted and impelled with the full power of the ventricle. After all, it is in the capillaries that the blood performs its functions; and here we should have a constant supply of the fluid in proper quantity and in proper condition to meet the nutritive and other requirements of the parts.

The elasticity of the arteries favors the flow of blood toward the capillaries by a mechanism which is easily understood. The blood discharged from the heart distends the elastic vessel, which reacts, after the distending force ceases to operate, and compresses its fluid contents. This reaction would have a tendency to force the blood in two directions, were it not for an instantaneous closure of the valves, which renders regurgitation with the heart impossible. The influence, then, can only be exerted in the direction of the periphery; and, if we can imagine as divided an action which is propagated with such rapidity, the reaction of that portion of the vessel immediately distended by the heart distends a portion farther on, which, in its turn, distends another portion, and so the wave passes along until the blood is discharged into the capillaries. In this way we can see that, in vessels removed a sufficient distance form the heart, the force exerted on the blood by the reaction of the elastic walls is competent to produce a very considerable current during the intervals of the heart's action. This theoretical view is fully carried out by the following simple and conclusive experiment of Marey: He connected two tubes of equal size, one of rubber and the other of glass, with the stop-cock of a large vase filled with water. The elastic tube was provided with a valve near the stop-cock, which prevented the reflux of fluid, and both were fitted with tips of equal caliber. When, by alternately opening and closing the stop-cock, water was allowed to flow into these tubes in an intermittent stream, it was found that a greater quantity was

FIG. 21.—*Apparatus for showing the action of the elasticity of the arteries.* (Marey.) V, vessel of water; R, stop-cock; T, double tube; S, valve; *a*, *a*, glass tube; *b*, *b*, rubber tube.

discharged by the elastic tube; but an equal quantity was discharged by both tubes when the stop-cock was left open and the fluid allowed to pass in a continuous stream. This simple experiment shows that not only does the elasticity of the arteries convert the intermittent current in the largest vessels into a current more and more nearly continuous as we approach the periphery, but that when reflux is prevented, as it is by the semilunar valves, the resiliency of the arteries assists the circulation.

Contractility of the Arteries.—It is a well-established anatomical fact that the medium-sized and smallest arteries contain contractile elements; and it is also a fact, proven by actual experiment, that, as a consequence of the condition of these fibres, the vessels undergo considerable variation in their caliber. The opinions of the older physiologists on this question have only an historical interest and will not, therefore, be discussed. Among the more recent investigations on this subject, we have the experiments of Cl. Bernard and of Schiff, which have been repeatedly confirmed, showing that, through the nervous system, the muscular coats of arteries may be readily made to contract or become relaxed. If the sympathetic be divided in the neck of a rabbit, in a very few minutes the arteries of the ear on that side are notably dilated. If the divided extremity of the nerve be galvanized, the vessels soon take on contraction and may become smaller than on the opposite side. These experiments demonstrate, in the most conclusive manner, the contractile properties of the small arteries and give us an idea how the supply of blood to any particular part may be regulated. The vessels may be most effectually excited through the nervous system; and it is on account of the difficulty in producing marked results by direct irritation, that the older physiologists were divided on the subject of their "irritability."

The contractility of the arteries has great physiological importance. As their function is simply to supply blood to the various tissues and organs, it is evident that, when the vessels going to any particular part are dilated, the supply of blood is necessarily increased. This is particularly well marked in the glands, which, during the intervals of secretion, receive a comparatively small quantity of blood. Bernard has shown that galvanization of what he calls the motor nerve of a gland dilates the vessels, largely increases the supply of blood, and induces secretion; while galvanization of the sympathetic filaments contracts the vessels, diminishes the supply of blood, and arrests secretion. The pallor of parts exposed to cold, and the flush produced by heat, are due, on the one hand, to contraction, and on the other, to dilatation of the small arteries. Pallor and blushing from mental emotions are examples of the same kind of action.

The ulterior effects on nutrition, which result from dilatation of the vessels of a part, are of great interest. When the supply of blood is much increased, as in section of the sympathetic in the neck, nutrition is exaggerated, and the temperature of the part is raised beyond that of the rest of the body.

The idea, which at one time obtained, that the arteries were the seat of rhythmical contractions which had a favorable influence on the current of blood is entirely erroneous.[1] It is hardly necessary to repeat that the prime cause of the arterial circulation is the force of the left ventricle. We have seen that the elasticity of the arteries produces a flow during the intervals of the heart's action, and the question now arises whether the force thus exerted be simply a return of the force required to expand the vessels, which has been borrowed, as it were, from the heart, or something superadded to the force of the heart. The experiment of Marey, already alluded to, settles this question. When water was forced in an intermittent current into two tubes, one elastic and the other inelastic but discharging by openings of equal size, by far the greater quantity was discharged by the elastic tube. A little reflection will show how the action of the elastic arteries must actually assist the circulation. The resiliency of the vessel is continually pressing their contents toward the periphery, as regurgitation is rendered impossible by the closure of the semilunar valves. The dilatation of the vessels with each systole of course admits an increased quantity of blood; and it has been experimentally demonstrated that the same intermittent force exerted on an inelastic tube will discharge a less quantity of liquid from an opening of equal caliber.

Superadded, then, to the direct action of the heart, we must recognize, as a cause influencing the flow of blood in the arteries, the resiliency of the vessels, especially of those of large size, this force being derived originally from the heart. Thus it will be seen that the arteries are constantly kept distended with blood by the heart; and, by virtue of their elasticity and the progressive increase in the capacity of this system as they branch, the powerful contractions of the central organ only serve to keep up an equable current in the capillaries. The small vessels, by virtue of their contractile walls, regulate the distribution of the blood, acting as the guards or sentinels of the process of nutrition, and, in fact, of all the numerous functions in which the blood is concerned.

Locomotion of the Arteries and Production of the Pulse.—At each contraction of the heart, the arteries are increased in length and many of them undergo a considerable locomotion. This may be readily observed in vessels which are tortuous in their course and is frequently very marked in the temporal artery in old persons. The elongation may also be seen if we watch attentively the point where an artery bifurcates, as at the division of the common carotid. It is simply the mechanical effect of sudden distention, which, while it increases the caliber of the vessel, causes an elongation even more marked.

The finger placed over an exposed artery or one which lies near the surface experiences a sensation at every beat of the heart as though the vessel were striking against it. This has long been observed and is called the pulse. Ordinarily it is appreciated when the current of blood is subjected to a certain amount of obstruction, as in the radial,

[1] Schiff has noticed rhythmical contractions in the superficial arteries of the ear in the rabbit and in some other animals; but this phenomenon is exceptional, and the movements do not appear to favor the current of blood. The recent experiments of Dr. J. J. Mason, of New York, show conclusively, to our mind at least, that there is not a peristaltic action of the muscular coats of the small arteries, capable of assisting the circulation. This view, however, is opposed to the ideas of Legros and Onimus and of some other physiologists.

which can readily be compressed against the bone. In an artery imbedded in soft parts which yield to pressure, the actual dilatation of the vessel being very slight, pulsation is felt with difficulty, if at all. When obstruction of an artery is complete, as in ligation of a vessel, the pulsation above the point of ligature is very marked and can be readily appreciated by the eye. The explanation of this exaggeration of the movement is the following: Normally, the blood passes freely through the arteries and produces, in the smaller vessels, very little movement or dilatation; when, however, the current is obstructed, as by ligation or even compression with the finger, the force of the heart is not sent through the vessel to the periphery but is arrested and therefore becomes more marked and easily appreciated. In vessels which have become undilatable and incompressible from calcareous deposits, the pulse cannot be felt. The character of the pulse indicates, to a certain extent, the condition of the heart and vessels. We have spoken, when treating of the heart, of the varying rapidity of the pulse, as it is a record of the rapidity of the action of this organ; but it remains for us to consider the mechanism of its production and its various characters.

Under ordinary circumstances, the pulse may be felt in all arteries which are exposed to investigation; and, as it is due to the movement of the blood in the vessels, the prime cause of its production is the contraction of the left ventricle. The experiments of Marey have shown that the impulse given to the blood by the heart is not felt in all the vessels at the same instant. By ingenious contrivances, which will be described farther on, this observer has succeeded in registering simultaneously the impulse of the heart, the pulse of the aorta, and the pulse of the femoral artery. He has thus ascertained that the contraction of the ventricle is anterior, in point of time, to the pulsation of the aorta, and that the pulsation of the aorta precedes the pulse in the femoral. This only confirms the views of other physiologists, particularly Weber, who described this progressive retardation of the pulse as we recede from the heart, estimating the difference between the ventricular systole and the pulsation of the artery in the foot at one-seventh of a second.

It is evident from what we know of the variations which occur in the force of the heart's action, the quantity of blood in the vessels, and from the changes which may take place in the caliber of the arteries, that the characters of the pulse must be subject to numerous variations. Many of these may be appreciated simply by the sense of touch. We find writers treating of the soft and compressible pulse, the hard pulse, the wiry pulse, the thready pulse, etc., as indicating various conditions of the circulatory system. The character of the pulse, aside from its frequency, has always been regarded as of great importance in disease; and the variations which occur in health form a most interesting subject for physiological inquiry.

Form of the Pulse.—It is evident that few of the characters of a pulsation, occupying as it does but one-seventieth part of a minute, can be ascertained by the sense of touch alone. This fact has been appreciated by physiologists; and, within the last few years, in order to accurately study this important subject, instruments for registering the pulse have been constructed, to enable us to analyze the dilatation and movements of the vessels. The idea of such an instrument was probably suggested by the following simple observation: When the legs are crossed, with one knee over the other, the beating of the popliteal artery will produce a marked movement in the foot. If we could apply to an artery a lever provided with a marking point in contact with a slip of paper moving at a definite rate, this point would register the movements of the vessel and its changes in caliber. The first physiologist who put this in practice was Vierordt, who constructed quite a complex instrument, so arranged that the impulse from an accessible artery, like the radial, was conveyed to a lever, which marked the movement upon a revolving cylinder of paper. This instrument was called a "sphygmograph." The traces made by it were perfectly regular and simply marked the extremes of dilatation, exaggerated, of course, by the length of the lever, and the number of pulsations in a given time. The latter can be easily estimated by more simple means; and, as the former did not convey any very definite physiological idea, the apparatus was regarded rather as a curiosity than an instrument for accurate research.

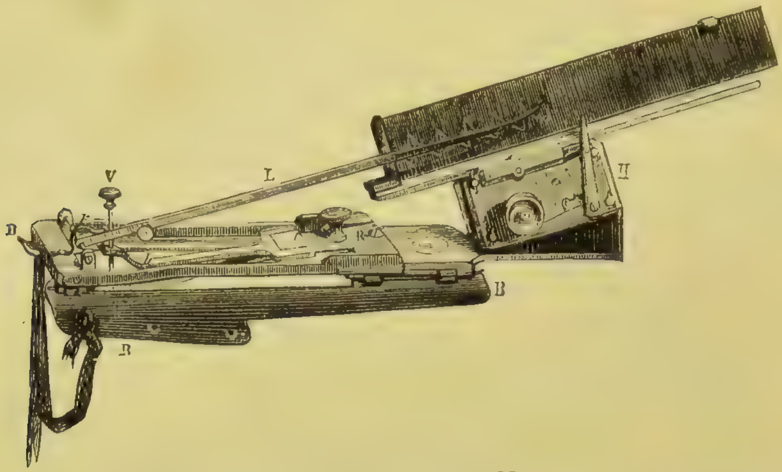


FIG. 22.—*Sphygmograph of Marey.*

The apparatus is securely fixed on the forearm, so that the spring under the screw V is directly over the radial artery. The movements of the pulse are transmitted to the long and light wooden lever L and registered upon the surface P, which is moved at a known rate by the clock-work H. The apparatus is so adjusted that the movements of the vessel are accurately amplified and registered by the extreme point of the lever.

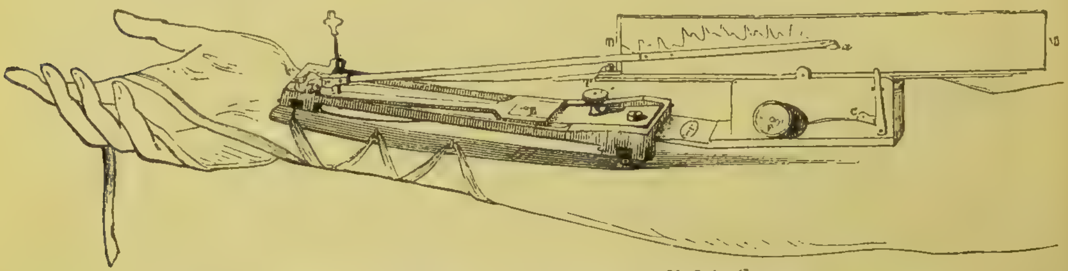


FIG. 23 (A).—*Sphygmograph of Marey applied to the arm.*

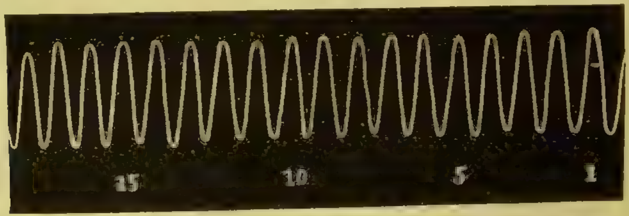


FIG. 23 (B).—*Trace of Vierordt.*

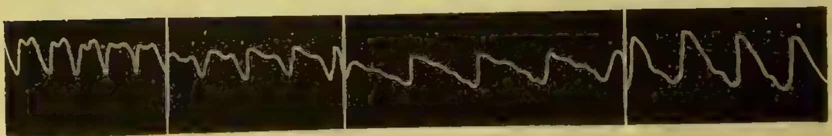


FIG. 23 (C).—*Trace of Marey.*
Portions of four traces taken in different conditions of the pulse.

The principle on which the instrument of Vierordt was constructed was correct; and it only remained to construct one which would be easy of application and produce a trace representing the shades of dilatation and contraction of the vessels, in order to lead to important practical results. These indispensable conditions are fully realized in the sphygmograph of Marey, to whose researches on the circulation we have repeatedly referred. The instrument simply amplifies the changes in the caliber of the vessel; and, although its application is, perhaps, not so easy as to make it generally useful in practice, in the hands of Marey it has given us a definite knowledge of the physiological character of the pulse and its modifications in certain diseases, information which is exceedingly desirable and which could not be arrived at by other means of investigation. In short, its mechanism is so accurate that, when skilfully used, it gives on paper the actual "form of the pulse." This instrument, applied to the radial artery, gives a trace very different from that obtained by Vierordt, which was simply a series of regular elevations and depressions. A comparison of the traces obtained by these two observers gives an idea of the defects which have been remedied by Marey; for it is evident that the dilatation and contraction of the arteries cannot be so regular and simple as would be inferred merely from the trace made by the instrument of Vierordt.

Analyzing the traces of Marey, we see that there is a dilatation following the systole of the heart, marked by an elevation of the lever, more or less sudden, as indicated by the angle of the trace, and of greater or less amplitude. The dilatation, having arrived at its maximum, is followed by reaction, which may be slow and regular, or may be, and generally is, interrupted by a second and slighter upward movement of the lever. This second impulse varies very much in amplitude. In some rare instances, it is nearly as marked as the first and may be appreciated by the finger, giving the sensation of a double pulse following each contraction of the heart. This is called the dicrotic pulse. As a rule, the first dilatation of the vessel is sudden and is indicated by an almost vertical line; this is followed by a slow reaction, indicated by a gradual descent of the trace, which is not, however, absolutely regular, but is marked by a slight elevation indicating a second impulse. The amplitude of the trace, or the distance between the highest and the lowest points marked by the lever, depends upon the amount of constant tension of the vessels. Marey has found that the amplitude is in an inverse ratio to the tension; which is very easily understood, for, when the arteries are but little distended, the force of the heart must be more marked in its effects than when the pressure of blood is very great. Any circumstance which facilitates the flow of blood from the arteries into the capillaries will, of course, relieve the tension of the arterial system, lessen the obstacle to the force of the heart, and increase the amplitude of the pulsation, and *vice versa.* In support of this view, Marey has found that cold applied to the surface of the body contracting, as it does, the smallest arteries, increases the arterial tension and diminishes the amplitude of the pulsation, while a moderate elevation of temperature produces an opposite effect.

In nearly all the traces given by Marey, the descent of the lever indicates more or less oscillation of the mass of blood. The physical properties of the larger arteries render this inevitable. As they yield to the distending influence of the heart, reaction occurs after this force is taken off and, if the distention be very great, gives a second impulse to the blood. This is quite marked, unless the tension of the arterial system be so great as to offer too much resistance. One of the most favorable conditions for the manifestation of dicrotism is diminished tension, which is always found coexisting with a very marked exhibition of this phenomenon.

The delicate instrument employed by Marey enabled him to accurately determine and register these various phenomena, by observations on the arteries of the human subject and the lower animals; and, by means of an ingeniously constructed "*schema*," representing the arterial system by elastic tubes and the left ventricle by an elastic bag provided with valves and acting as a syringe, he satisfactorily established the conditions of tension, etc., necessary to their production. In this *schema*, the registering apparatus, simpler in construction than the sphygmograph, could be applied to the tubes with more accuracy and ease. He demonstrated, by experiments with this system of tubes, that the amplitude of the pulsations, the force of the central organ being the same, is greatest when the tubes are moderately distended, or when the tension of fluid is low, and *vice versa*. He demonstrated, also, that a low tension favors dicrotism. In this latter observation, he diminished the tension by enlarging the orifices by which the fluid was discharged from the tubes, imitating the dilatation of the small vessels, by which the tension is diminished in the arterial system. He also demonstrated that an important and essential element in the production of dicrotism is the tendency to oscillation of the fluid in the vessels during the intervals between the contractions of the heart. This can only occur in a fluid which has a certain weight and acquires a velocity from the impulse; for, when air was introduced into the apparatus, dicrotism could not be produced under any circumstances, as the fluid did not possess weight enough to oscillate between the impulses. Water produced a well-marked dicrotic impulse under favorable conditions; and with mercury, the oscillations made two, three, or more distinct impulses. By these experiments he proved that the blood oscillates in the vessels, if this movement be not suppressed by too great pressure or tension. This oscillation gives the successive rebounds that are marked in the descending line of the pulse, and is capable, in some rare instances when the arterial tension is very slight, of producing a second rebound of sufficient force to be appreciated by the finger.

Without treating of the variations in the character of the pulse in disease, due to the action of the muscular coat, we shall consider some of the external modifying influences which come within the range of physiology. The smallest vessels and those of medium size possess to an eminent degree what is called tonicity, or the property of maintaining a certain continued amount of contraction. This contraction is antagonistic to the distending force of the blood, as is shown by opening a portion of an artery included between two ligatures in a living animal, when the contents will be forcibly discharged and the caliber of that portion of the vessel is very much diminished. Too great distention of the vessels by the pressure of blood seems to be prevented by this constant action of the muscular coat; and thus the conditions are maintained which give the pulse the characters we have just described.

By excessive and continued heat, the muscular tissue of the arteries may be dilated so as to offer less resistance to the distending force of the heart. Under these circumstances, the pulse, as felt by the finger, will be found to be larger and softer than normal. Cold, either general or local, has an opposite effect; the arteries become contracted, and the pulse assumes a harder and more wiry character. Usually, prolonged contraction of the arteries is followed by relaxation, as is seen in the full pulse and glow of the surface which accompany reaction after exposure to cold.

It has been found, also, that there is a considerable difference in the caliber of the arteries at different periods of the day. The diameter of the radial has been found very much greater in the evening than in the morning, producing, naturally, a variation in the character of the pulse. We learn from these physiological variations, how, in disease, when they become more considerable, they may give important information with regard to the condition of the system.

Pressure of Blood in the Arteries.

The reaction of the elastic walls of the arteries during the intervals of the heart's action gives rise to a certain amount of constant pressure, by which the blood is continually forced toward the capillaries. The discharge of blood into the capillaries has a constant tendency to diminish this pressure; but the contractions of the left ventricle, by forcing repeated charges of blood into the arteries, have a compensating action. By the equilibrium between these two agencies, a certain degree of tension is maintained in the arteries, which is called the arterial pressure.

The first experiments with regard to the extent of the arterial pressure were made by Hales, an English physiologist, more than a hundred years ago. This observer, adapting a long glass tube to the artery of a living animal, ascertained the height of the column of blood which could be sustained by the arterial pressure. In some experiments on the carotid of the horse, the blood mounted to the height of from eight to ten feet.

All experiments on the arterial pressure are made on the principle of the experiment of Hales, which, with reference simply to the constant pressure in the arteries, is as useful as those of later date and much more striking. The only inconvenience is in the manipulation of the long tube; but this may be avoided by setting it in a strip of wood, when it can be easily handled. If a large artery, as the carotid, be exposed in a living animal, and a metallic point, connected with a vertical tube of small caliber and from seven to eight feet long by a bit of elastic tubing, be secured in the vessel, the blood will rise to the height of about six feet and remain at this point almost stationary, indicating, by a slight pulsatile movement, the action of the heart. On carefully watching the level in the tube, in addition to the rapid oscillation coincident with the pulse, another oscillation will be observed, which is less frequent and which corresponds with the movements of respiration. The pressure, as indicated by an elevation of the fluid, is slightly increased during expiration and diminished during inspiration.[1]

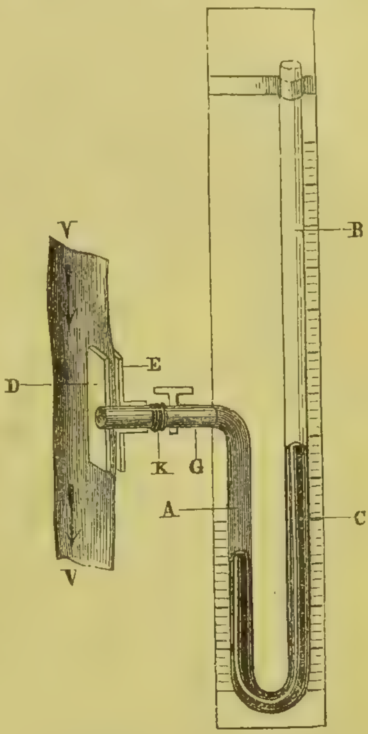


FIG. 24.—*Hæmadynamometer of Poiseuille, modified by Ludwig, Spengler, and Valentin.*

The instrument is connected with the vessel V V, in such a manner that the circulation is not interrupted. The elevation of the mercury in the branch B C indicates the amount of pressure.

The experiment with the long tube gives us the best general idea of the arterial pressure, which will be found to vary between five and a half and six feet of blood, or a few inches more of water. The oscillations produced by the contractions of the heart are not very marked, on account of the great friction in so long a tube; but this is favorable to the study of the constant pressure. It has been found that the estimates above given do not vary very much in animals of different sizes. Bernard found the pressure in the carotid of a horse but little more than in the dog or rabbit. In the larger animals, it is the force of the heart which is increased, and not, to any considerable extent, the constant pressure in the vessels.

The experiments of Hales were made with a view of calculating the force of the heart and were not directed particularly to the conditions and variations of the arterial pressure. It is only since the experiments performed by Poiseuille with the hæmadynamometer, in 1828, that we have any reliable data on this latter point. Poiseuille's instrument for measuring the force of the blood is a simple graduated U-tube, half filled with mercury, with one arm bent at a right angle, so that it can easily be connected with the artery. The pressure of the blood is indicated by a depression in the level of the mercury on one side and a corresponding elevation on the other. This instrument is generally considered as possessing great advantages over the long glass tube; but, for estimating simply the arterial pressure, it is much less useful, as it is more sensitive to the impulse of the heart. For the study of the cardiac pressure, it has the disadvantage, in the first place, of considerable friction, and, again, the weight of the column of mercury produces an extent of oscillation by its mere impetus, greater than that which would actually represent the force of the heart.

An important improvement in the hæmadynamometer was made by Magendie. This apparatus, the cardiometer, in which Bernard has made some important modifications, is

[1] In all these experiments on the arterial or cardiac pressure, it is necessary to fill part of the tube, or whatever apparatus we may use, with a solution of carbonate of soda, in order to prevent coagulation of the blood as it passes out of the vessels.

the one now generally used. It consists of a small but thick glass bottle, with a fine, graduated glass tube about twelve inches in length, communicating with it, either through the stopper or by an orifice in the side. The stopper is pierced by a bent tube which is to be connected with the blood-vessel. The bottle is filled with mercury so that it will rise in the tube to a point which is marked zero. It is evident that the amount of pressure on the mercury in the bottle will be indicated by an elevation in the graduated tube; and, moreover, from the fineness of the column in the tube, we avoid some of the inconveniences which are due to the weight of mercury in the hæmadynamometer, and we also have less friction. This instrument is appropriately called the cardiometer, as it indicates most accurately, by the extreme elevation of the mercury, the force of the heart;

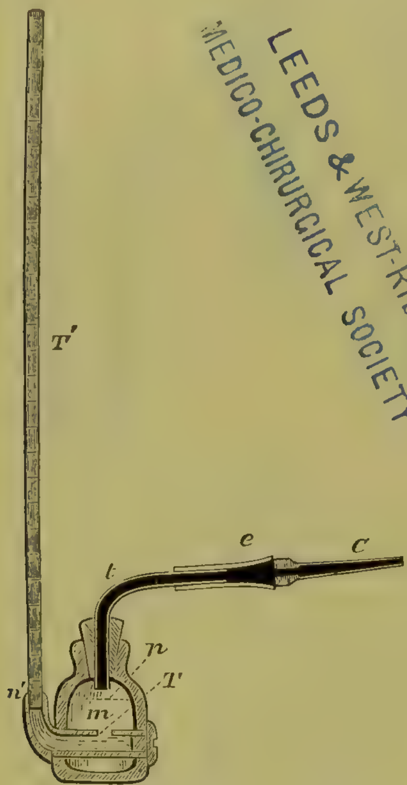


FIG. 25 (A).—*Section of the cardiometer of Magendie, as modified by Bernard.*

A strong glass bottle is perforated at each side and fitted with an iron tube, with an opening, T, by which the mercury enters. One end of the iron tube is closed, and the other is bent upward and connected with the graduated glass tube T′, which has a caliber of from $\frac{1}{12}$ to $\frac{1}{8}$ of an inch. The bottle is filled with mercury until it rises to *n′* in the tube which is marked zero. The cork is perforated by the tube *t*, which is connected by a rubber tube with the point C, which is introduced into the vessel.

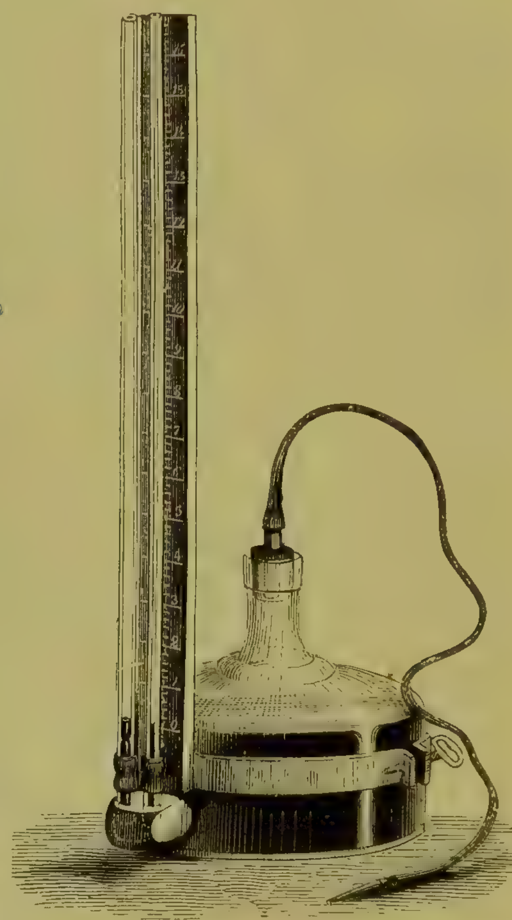


FIG. 25 (B).—*Compensating instrument of Marey.*

but it is not as perfect in its indications of the mean arterial pressure, for, in the abrupt descent of the mercury during the diastole of the heart, the impetus causes the level to fall considerably below the real standard of the constant pressure. Marey has succeeded in correcting this difficulty in what he calls the "compensating" instrument, which is constructed on the following principle: Instead of a simple glass tube which communicates with the mercury in the bottle, as in Magendie's cardiometer, he has two tubes, one of which is like the one already described and represents oscillations produced by the heart, while the other is larger, and has, at the lower part, a constriction of the caliber, which is here reduced to capillary fineness. The latter tube is designed to give the mean arterial pressure; the constricted portion offering such an obstacle to the rise of the mercury that the intermittent action of the heart is not felt, the mercury rising slowly to a certain level, which is constant and varies only with the constant pressure in the vessels.

We have only an approximative idea of the average pressure in the arterial system in the human subject, deduced from experiments on animals. It has already been stated to be equal to about six feet of water or six inches of mercury.

The most interesting questions connected with the subject of the arterial pressure are the comparative pressure in different parts of the arterial system, the conditions which modify the arterial pressure, and its influence on the pulse. These points have all been pretty fully investigated by experiments on animals and observations on systems of elastic tubes arranged to represent the blood-vessels.

Pressure in Different Parts of the Arterial System.—The experiments of Hales, Poiseuille, Bernard, and others, seem to show that the constant arterial pressure does not vary in arteries of different sizes. These physiologists have experimented particularly on the carotid and crural, and have found the pressure in these two vessels about the same. From their experiments they conclude that the force is equal in all parts of the arterial system. The experiments of Volkmann, however, have shown that this conclusion has been too hasty. With the registering apparatus of Ludwig, he has taken the pressure in the carotid and the metatarsal arteries and has always found a considerable difference in favor of the former. In an experiment on a dog, he found the pressure equal to one hundred and seventy-two millimeters in the carotid, and one hundred and sixty-five in the metatarsal. In an experiment on a calf, the pressure was one hundred and sixteen mm. in the carotid, and eighty-nine mm. in the metatarsal; and in a rabbit, ninety-one mm. in the carotid, and eighty-six mm. in the crural. These experiments show that the pressure is not absolutely the same in all parts of the arterial system, that it is greatest in the arteries nearest the heart, and that it gradually diminishes as we near the capillaries. The difference is very slight, almost inappreciable, until we come to vessels of very small size; but here the pressure is directly influenced by the discharge of blood into the capillaries. The cause of this diminution of pressure in the smallest vessels is the proximity of the great outlet of the arteries, the capillary system; for, as we shall see farther on, the flow into the capillaries has a constant tendency to diminish the pressure in the arteries. It is obvious that this influence can only be felt in a very marked degree in the vessels of smallest size.

Influence of Respiration.—It is easy to see, in studying the arterial pressure with any of the instruments we have described, that there is a marked increase with expiration and a diminution with inspiration. The fact that expiration will increase the force of the jet of blood from a divided artery has long been observed and accords perfectly with the above statement. In tranquil respiration, the influence upon the flow of blood is due simply to the mechanical action of the thorax. With every inspiration, the air-cells are enlarged, as well as the blood-vessels of the lungs, the air rushes in through the trachea, and the movement of the blood in the veins near the chest is accelerated. At the same time, the blood in the arteries is somewhat retarded in its flow from the thorax, or at least does not feel the expulsive influence which follows with the act of expiration. The arterial pressure at that time is at its minimum. With the expiratory act, the air is expelled by compression of the lungs, the flow of blood into the thorax by the veins is retarded to a certain extent, while the flow of blood into the arteries is favored. This is strikingly exhibited in the augmented force, with expiration, in the jet from a divided artery. Under these circumstances the arterial pressure is at its maximum. In perfectly tranquil respiration, the changes due to inspiration and expiration are slight, presenting a difference of not more than half an inch to an inch in the cardiometer. When the respiratory movements are exaggerated, the oscillations are very much more marked.

Interruption of respiration is followed by a very great increase in the arterial pressure. This is due, not to causes within the chest, but to obstruction to the circulation in the capillaries. We are already aware of the influence which the flow of blood into the capillaries is constantly exerting upon the arterial pressure. This tendency to diminish the quantity of blood in the arteries, and consequently the pressure, is constantly counteracted by the blood sent into the arteries by the contractions of the heart. With an interruption of the respiratory function, the non-aërated blood passes into the arteries but cannot flow readily through the capillaries; and, as a consequence, the arteries are abnormally distended and the pressure is greatly increased. If respiration be permanently arrested, the arterial pressure becomes, after a time, diminished below the normal standard, and is finally abolished, on account of the stoppage of the action of the heart. If respiration be resumed before the heart has become arrested, the pressure soon returns to its normal condition.

Muscular effort considerably increases the arterial pressure. This is due to two causes. In the first place, the chest is generally compressed, favoring the flow of blood into the great vessels. In the second place, muscular exertion produces a certain amount of obstruction to the discharge of blood from the arteries into the capillaries. Numerous experiments upon animals have shown a great increase in pressure in the struggles which occur during severe operations. It has been shown that galvanization of the sympathetic in the neck and irritation of certain of the cerebro-spinal nerves increase the arterial pressure, probably from an influence on the muscular coats of some of the arteries, causing them to contract and thereby diminishing the total capacity of the arterial system.

Effects of Hæmorrhage.—Diminution in the quantity of blood has a remarkable effect upon the arterial pressure. If, in connecting the instrument with the arteries, we allow even one or two jets of blood to escape, the pressure will be found diminished perhaps one-half, or even more. It is hardly necessary to discuss the mechanism of the effect of the loss of blood on the tension of the vessels, but it is wonderful how soon the pressure in the arteries regains its normal standard after it has been lowered by hæmorrhage. As the pressure depends largely upon the quantity of blood, as soon as the vessels absorb the serosities in sufficient quantity to repair the loss, the pressure is increased. This takes place in a very short time, if the loss of blood be not too great.

Experiments on the arterial pressure with the cardiometer have verified the fact stated in treating of the form of the pulse; namely, that the pressure in the vessels bears an inverse ratio to the distention produced by the contractions of the heart. In the cardiometer, the mean height of the mercury indicates the constant, or arterial pressure; and the oscillations, the distention produced by the heart. It is found that when the pressure is great, the extent of oscillation is small, and *vice versa*. It will be remembered that the researches of Marey demonstrated that an increase of the arterial pressure diminishes the amplitude of the pulsations, as indicated by the sphygmograph, and that the amplitude is very great when the pressure is slight. It is also true, as a general rule, that the force of the heart, as indicated by the cardiometer, bears an inverse ratio to the frequency of its pulsations.

Depressor Nerve of the Circulation—Within the last few years, an important discovery has been made by Cyon and Ludwig, of a nerve arising in the rabbit by two roots, one from the main trunk of the pneumogastric and the other from the superior laryngeal nerve, which joins the sympathetic filaments in the chest and passes to the heart. This nerve has a reflex action, as was shown by the experiments of Cyon, its galvanization reducing the arterial pressure by one-third or one-half. This action is known to be reflex, for, when the nerve is divided, galvanization of the central end affects the arterial pressure, while no such result follows stimulation of the peripheral extremity; and the effect is manifested when the pneumogastrics have been divided and no direct nervous influence is exerted over the heart. It is thought that the reduction in the arterial pressure following galvanization of the so-called depressor nerves is mainly due to the action of the splanchnic nerves, by which the abdominal vessels become largely dilated. If the abdomen be opened and one or more of the splanchnic nerves be divided, the arterial pressure is immediately diminished, and the pressure is restored if the divided ends of the nerves be galvanized. If, after division of the splanchnic nerves and the consequent diminution of the arterial pressure, the depressor nerves be galvanized, the pressure still undergoes some additional diminution, but this is much less than the diminution which follows galvanization of the depressor nerves without section of the splanchnic. The action of these nerves will be more fully considered in connection with the physiology of the nervous system.

Rapidity of the Current of Blood in the Arteries.—The question of the rapidity of the arterial circulation has long engaged the attention of physiologists; but the experiments of Volkmann, with his hæmadrometer, and of Vierordt, with a peculiar instrument which he devised for the purpose, did not lead to results that were entirely satisfactory.

The best instrument for measuring the rapidity of the circulation in the arteries was devised by Chauveau, of the Veterinary School at Lyons. This will give, by calculation, the actual rapidity of the circulation; and, what is more interesting, it marks accurately the rapid variations in velocity which occur at different periods of the heart's action.

The instrument to be applied to the carotid of the horse consists of a thin brass tube, about an inch and a half in length and of the diameter of the artery (about three-eighths of an inch), which is provided with an oblong, longitudinal opening, or window, near the middle, about two lines long and one line wide. A piece of thin vulcanized rubber is wound around the tube and firmly tied so as to cover this opening. Through a transverse slit in the rubber, is introduced a very light metallic needle, an inch and a half in length and flattened at its lower part. This is made to project about half-way into the caliber of the tube. A flat, semicircular piece of metal, divided into an arbitrary scale, is attached to the tube, to indicate the deviations of the point of the needle.

The apparatus is introduced carefully into the carotid of a horse, by making a slit in the vessel, introducing first one end of the tube directed toward the heart, then allowing a little blood to enter the instrument, so as to expel the air, and, when full, introducing the other end, securing the whole by ligatures above and below.

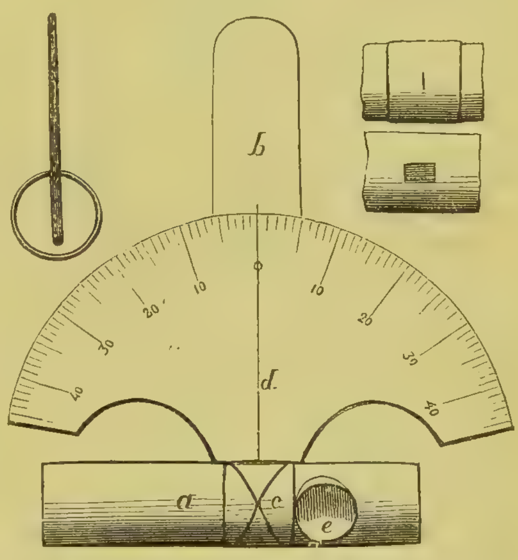


Fig. 26.—*Chauveau's instrument for measuring the rapidity of the flow of blood in the arteries.*

The instrument viewed in face—*a*, the tube to be fixed in the vessel; *b*, the dial which marks the extent of movement of the needle *d*; *e*, a lateral tube for the attachment of a cardiometer, if desired.

When the circulation is arrested, the needle should be vertical, or mark zero on the scale. When the flow is established, a deviation of the needle occurs, which varies in extent with the rapidity of the current. Having removed all pressure from the vessel so as to allow the current to resume its normal character, the deviations of the needle are carefully noted, as they occur with the systole of the heart, with the diastole, etc. After withdrawing the instrument, it is applied to a tube of the size of the artery, in which a current of water is made to pass with a rapidity which will produce the same deviations as occurred when the instrument was connected with the blood-vessel. The rapidity of the current in this tube may be easily calculated by receiving the fluid in a graduated vessel and noting the time occupied in discharging a given quantity. By this means we ascertain the rapidity of the current of blood. This instrument is on the same principle as the one constructed by Vierordt, but in sensitiveness and accuracy it is much superior. In the hands of Chauveau, the results, particularly those with regard to variations in the rapidity of the current, are very interesting.

Rapidity of the Current in the Carotid.—It has been found that three currents, with different degrees of rapidity, may be distinguished in the carotid:

1. At each ventricular systole, we have, as the average of the experiments of Chauveau, the blood moving in the carotids at the rate of $20\frac{4}{10}$ inches per second. After this, the rapidity quickly diminishes, the needle returning quite or nearly to zero, which would indicate complete arrest.

2. Immediately succeeding the ventricular systole, we have a second impulse given to the blood, which is synchronous with the closure of the semilunar valves, the blood moving at the rate of $8\frac{6}{10}$ inches per second. Chauveau calls this the dicrotic impulse.

3. After the dicrotic impulse, the rapidity of the current gradually diminishes, until just before the systole of the heart, when the needle is nearly at zero. The average rate, after the dicrotic impulse, is $5\frac{9}{10}$ inches per second.

The above experiments give us, for the first time, correct notions of the rapidity and variations in the flow of blood in the larger vessels; and it is seen that they correspond in a remarkable degree with the experiments of Marey on the form of the pulse. Marey showed that there is a marked oscillation of the blood in the vessels, due to a reaction of their elastic walls, following the first violent distention by the heart; that, at the time of closure of the semilunar valves, the arteries experience a second, or dicrotic distention, much less than the first; and, following this, there is a gradual decline in the distention until the minimum is reached. Chauveau shows by experiments with his instrument that, corresponding to the first dilatation of the vessels, the blood moves with great rapidity; following this, the current suddenly becomes nearly arrested; this is followed by a second acceleration in the current, less than the first; and, following this, we have a gradual decline in the rapidity up to the time of the next pulsation.

Rapidity in Different Parts of the Arterial System.—From the fact that the arterial system increases in capacity as we recede from the heart, we should expect to find a corresponding diminution in the rapidity of the flow of blood. There are, however, many circumstances, aside from simple increase in the capacity of the vessels, which modify the blood-current and render inexact any calculations made upon purely physical principles. Such are the tension of the blood, the conditions of contraction or relaxation of the smallest arteries, etc. It is necessary, therefore, to have recourse to actual experiments to arrive at any definite results on this point. The experiments of Volkmann showed a great difference in the rapidity of the current in the carotid and metatarsal arteries, the averages being 10 inches per second in the carotid and 2·2 inches in the metatarsal. The same difference, although not quite so marked, was found by Chauveau between the carotid and the facial. The last-named observer also noted an important modification in the character of the current in the smaller vessels. As we recede from the heart, the systolic impulse becomes rapidly diminished, being reduced in one experiment about two-thirds; the dicrotic impulse becomes feeble or may even be abolished; but the constant flow is very much increased in rapidity. This fact coincides with the ideas already advanced with regard to the gradual conversion, by virtue of the elasticity of the vessels, of the impulse of the heart into, first, a remittent, and, in the very smallest arteries, a nearly constant current.

The rapidity of the flow in any artery must be subject to constant modifications due to the condition of the arterioles which are supplied by it. When these little vessels are dilated, the artery of course empties itself with greater facility, and the rapidity is increased. Thus the rapidity bears a relation to the arterial pressure; as, independently of a diminution in the entire quantity of the circulating fluid, variations in the pressure depend chiefly on causes which facilitate or retard the flow of blood into the capillaries. A good example of enlargement of the capillaries of a particular part is in mastication, when the salivary glands are brought into activity and the quantity of blood which they receive is greatly increased. Chauveau found an immense increase in the rapidity of the flow in the carotid of a horse during mastication. The enlargement of the vessels of the glands during their function has been conclusively proven by the experiments of Bernard. It must be remembered that, in all parts of the arterial system, the rapidity of the current of blood is constantly liable to increase from dilatation of the small vessels and to diminution from their contraction.

Circulation of the Blood in the Capillaries.

Before entering upon the study of the capillary circulation, we should define what we mean by the capillary vessels as distinguished from the smallest arteries and veins. From a strictly physiological point of view, the capillaries are to be regarded as commencing

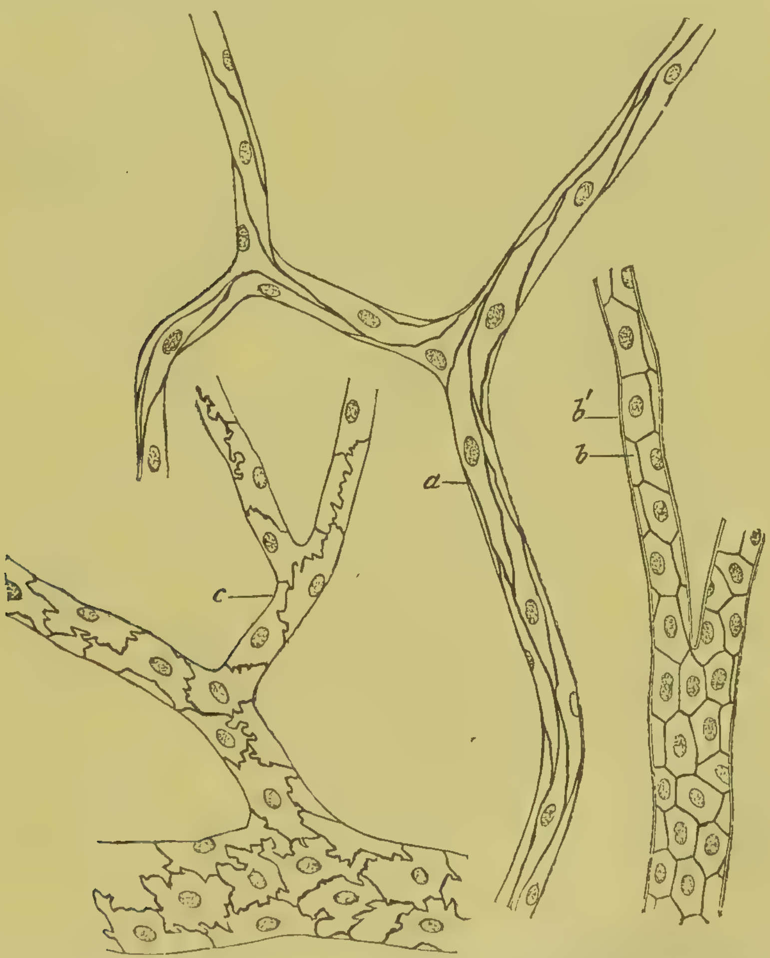


FIG. 27.—*Capillary blood-vessels from the pecten of the eye of the bird.* (Eberth.)
a, small capillaries, with fusiform cells; *b*, capillaries with polygonal cells; *b′*, hyaloid membrane investing the capillaries; *c*, capillaries from the intestine of the snail.

at the point where the blood is brought near enough to the tissues to enable them to separate the elements necessary for their regeneration and to give up the products of their physiological decay. With our present knowledge, it is impossible to assign any limit where the vessels cease to be simple carriers of blood; and it does not seem probable that it will ever be known to what part of the vascular system the processes of nutrition are exclusively confined. The divisions of the blood-vessels must be, to a certain extent, arbitrarily defined; and we should feel at liberty to adopt the views of any reliable observer with regard to the kind of vessels which are to be considered as capillaries. The most simple, and what seems to be the most physiological view, is to regard as capillaries those vessels which have but a single tunic; for, in these, the blood is brought in closest proximity to the tissues. Vessels which are provided, in addition, with a muscular or with muscular and fibrous coats are to be regarded either as small arteries or as venous radicles. This view is favored by the character of the currents of blood as seen in microscopical observation of the circulation in transparent parts. Here an impulse is observed with each contraction of the heart, until we come to vessels which have but one coat and are so narrow as to allow the passage of but a single line of blood-corpuscles.

Physiological Anatomy of the Capillaries.—If the arteries be followed out to their minutest ramifications, they will be found progressively diminishing in size as they branch, and their coats, especially the muscular, becoming thinner and thinner, until at last they present an internal structureless coat, lined by epithelium with oval, longitudinal nuclei, a middle coat, formed of but a single layer of circular muscular fibres, and an external coat, composed of a very thin layer of longitudinal fibres of the white inelastic tissue. These vessels are from $\frac{1}{400}$ to $\frac{1}{200}$ of an inch in diameter. They become smaller as they branch, and undoubtedly possess the property of contractility, which is particularly marked in the arterial system. Following the course of the vessels, when they are reduced in size to about $\frac{1}{800}$ of an inch, the external fibrous coat is lost, and the vessel then presents only the internal coat and a single layer of muscular fibres. These become smaller as they branch, finally lose the muscular coat, and have then but a single tunic. These last we shall consider as the true capillary vessels.

The minute structure of the capillary vessels is of considerable importance and interest and has been very closely investigated within the last few years. It was formerly thought that the smallest vessels, which we describe as the true capillaries, were composed of a single, homogeneous membrane, from $\frac{1}{25000}$ to $\frac{1}{2500}$ of an inch thick, with nuclei embedded in its substance, but not provided with an epithelial lining. Recent observations, however, have shown that the membrane is homogeneous, elastic, perhaps contractile, and, in some parts at least, is provided with fusiform or polygonal epithelium of excessive tenuity. The borders of the epithelial cells may be seen by staining the vessels with nitrate of silver. In the smallest capillaries, the cells are narrow and elongated or fusiform; and in the larger vessels, they are more polygonal, with very irregular borders. The nuclei which have been observed in the walls of the vessels belong to this layer of epithelium. By the same process of staining with nitrate of silver, we frequently observe irregular, non-nucleated areas; and it has been supposed by some that these indicate the presence of stomata, or orifices in the walls of the vessels. This latter point, however, has not been definitely determined. It cannot at present be stated positively whether or not orifices normally exist in the walls of the blood-vessels. Most of the anatomical points we have just mentioned have been developed by observations upon the vessels of the frog.

The diameter of the capillaries is generally as small as, or it may be smaller than that of the blood-corpuscles; so that these bodies always move in a single line and must become deformed in passing through the smallest vessels, recovering their natural shape, however, when they pass into vessels of larger size. The capillaries are smallest in the nervous and muscular tissue, retina, and patches of Peyer, where they have a diameter of from $\frac{1}{5000}$ to $\frac{1}{4000}$ of an inch. In the mucous layer of the skin and in the mucous membranes, they are from $\frac{1}{4000}$ to $\frac{1}{2400}$ of an inch in diameter. They are largest in the glands and bones, where they are from $\frac{1}{3000}$ to $\frac{1}{2000}$ of an inch in diameter. These measurements indicate the size of the vessels and not their caliber. Taking out the thickness of their walls, it is only the very largest of them that will admit of the passage of a blood-disk without a change in its form.

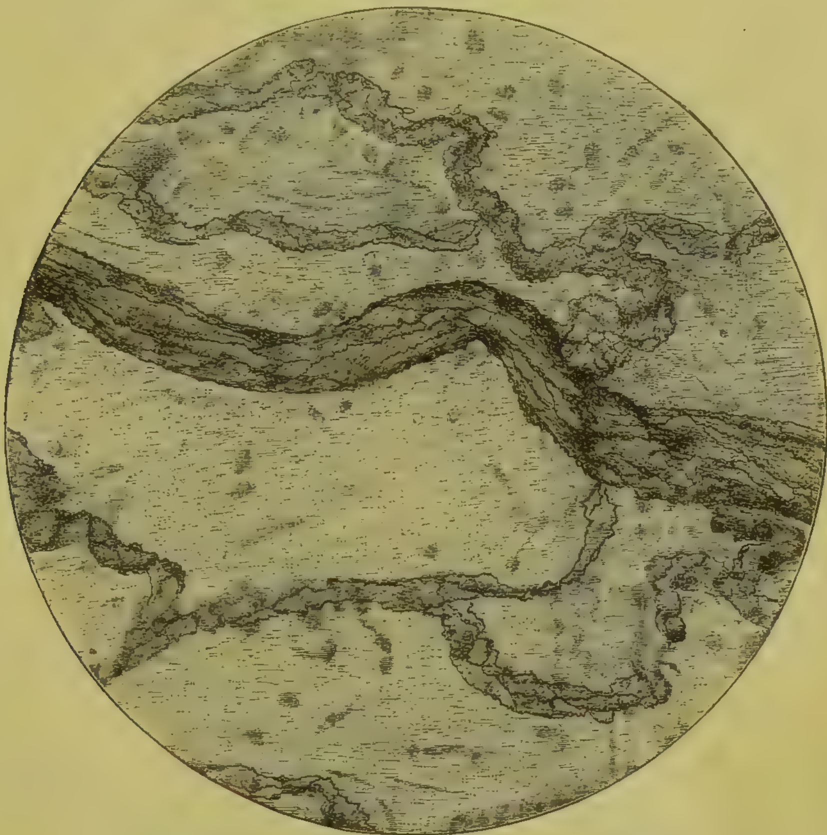


FIG. 28.—*Small artery and capillaries, from the muscular coats of the urinary bladder of the frog; magnified 400 diameters.* (From a photograph taken at the United States Army Medical Museum.)
This preparation shows the epithelium of the vessels. It is injected with nitrate of silver, stained with carmine, and mounted in Canada balsam.

Unlike the arteries, which grow smaller as they branch, and the veins, which become larger, as we follow the course of the blood, by union with each other, the capillaries form a true plexus of vessels of nearly uniform diameter, branching and inosculating in every direction and distributing blood to the parts as their physiological necessities demand. This mode of inosculation is peculiar to these vessels, and the plexus is rich in the tissues, as a general rule, in proportion to the activity of their nutrition. Although their arrangement presents certain differences in different organs, the capillary vessels have everywhere the same general characteristics, the most prominent of which are uniform diameter and absence of any positive direction. The net-work thus formed is very rich in the substance of the glands and in the organs of absorption; but the vessels are only distended with blood during the physiological activity of these parts. In the lungs, the meshes are particularly close. In other parts, the vessels are not so abundant, presenting great variations in different tissues. In the muscles and nerves, in which nutrition is very active, the supply is much more abundant than in other parts, like fibroserous membranes, tendons, etc. In none of the tissues do we find capillaries penetrating the anatomical elements, as the ultimate muscular or nervous fibres. Some tissues receive no blood, at least they contain no vessels which are capable of carrying red blood, and are nourished by imbibition of the nutrient plasma of the circulating fluid. Examples of these, which are called extra-vascular tissues, are cartilage, nails, and hair.

The foregoing anatomical sketch gives an idea of how near the blood is brought to the tissues in the capillary system, and how, once conveyed there by the arteries, and the supply regulated by the action of the muscular coat of the smaller vessels, the blood is distributed for the purposes of nutrition, secretion, absorption, exhalation, or whatever function the part has to perform. This will be still more apparent when we come to consider the course of the blood in the capillaries and the immense capacity of this system, as compared with the arteries or veins.

The capacity of the capillary system is immense. It is only necessary to consider the great vascularity of the skin, mucous membranes, or muscles, to realize this fact. In injections of these parts, it seems, on microscopical examination, as though they contained nothing but capillaries. In preparations of this kind, the elastic and yielding coats of the capillaries are distended to their utmost limit. Under some circumstances, in health, they are largely distended with blood, as the mucous lining of the alimentary canal during digestion, the whole surface presenting a vivid-red color, indicating the great richness of the capillary plexus. Various estimates of the capacity of the capillary, as compared with the arterial system, have been made, but they are simply approximative, and there seems to be no means by which an estimate, with any pretensions to accuracy, can be formed. The various estimates which are given are founded upon calculations from microscopical examinations of the rapidity of the capillary circulation as compared with the circulation in the arteries. In this way, it has been estimated that the entire capacity of the capillary system is from five hundred to eight hundred times that of the arterial system. It must be evident to any one who has witnessed the capillary circulation under the microscope, that the conditions under which the animal under examination is placed are liable to interfere with the current of blood; and the periodical congestion of certain parts, the fugitive flushes of the skin, the condition of the smallest arteries induced by changes of temperature, exercise, etc., make it evident that the current of blood is liable to great variations. It is impossible to strictly apply to the capillary circulation in the various parts of the human subject observations on the wing of a bat or the mesentery of a cat. We must consider, then, these estimates as mere suppositions, and they are given for what they are worth.

Phenomena of the Capillary Circulation.—The most convenient situation for the practical study of the capillary circulation is the tongue or the web of the frog. Here may be studied, not only the movement of the blood in the true capillaries, but the circulation in the smallest arteries and veins, the variations in caliber of these vessels, especially the arterioles, by the action of their muscular tunic, and, indeed, the action of vessels of considerable size. This has been a most valuable means of studying the circulation in the capillaries as contrasted with the flow in the small arteries and veins, and the only one, indeed, which could give us any definite idea of the action of these vessels.

The magnificent spectacle of the capillary circulation was first observed by Malpighi, in the lungs, and afterward by Leeuwenhoek, Spallanzani, Haller, Cowper, and others, in other parts. We see the great arterial rivers, in which the blood flows with wonderful rapidity, branching and subdividing, until the circulating fluid is brought to the network of fine capillaries, where the corpuscles dart along one by one. The blood is then collected by the veins and carried in great currents to the heart. This exhibition, to the student of Nature, is of inexpressible grandeur; and our admiration is not diminished when we come to study the phenomena in detail. We find here a subject as interesting as was the action of the heart when first seen by Harvey, involving some of the most important phenomena of the circulation. It can be seen how the arterioles regulate the supply of blood to the tissues; how the blood distributes itself by the capillaries; and, finally, having performed its office, how it is collected and carried off by the veins.[1]

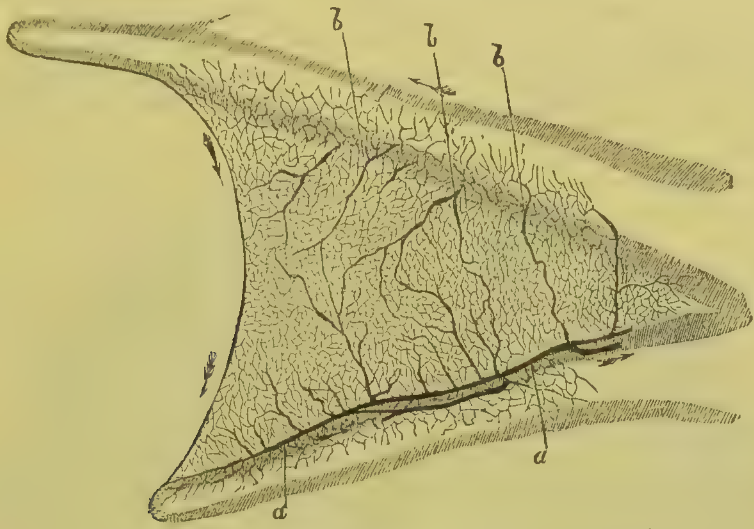


FIG. 29.—*Web of the frog's hind-foot; magnified.* (Wagner.)
a, *a*, veins; *b*, *b*, *b*, arteries.

In studying the circulation under the microscope, the anatomical division of the blood into corpuscles and a clear plasma is observed. This is peculiarly evident in cold-blooded animals, the corpuscles being comparatively large and floating in a plasma which forms a distinct layer next the walls of the vessel. The leucocytes, which are much fewer than the red corpuscles, are generally found in the layer of plasma.

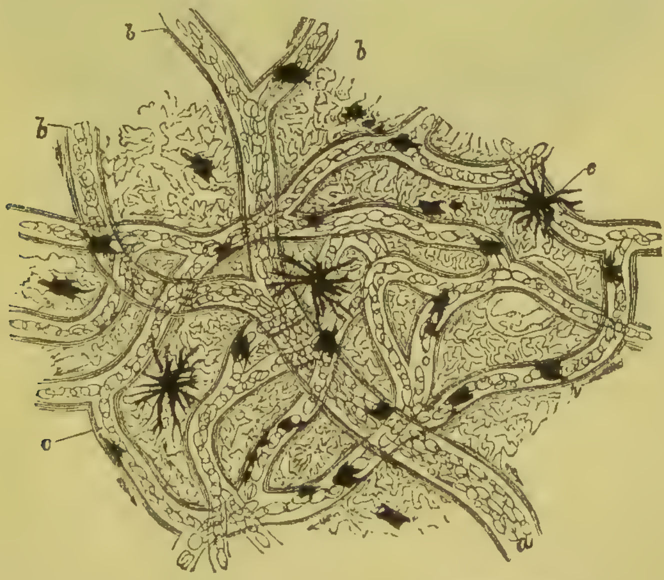


FIG. 30.—*Circulation in the web of the frog's foot.* (Wagner.)
The black spots, some of them star-shaped, are pigmentary matter. *a*, a venous trunk, composed of three principal branches (*b*, *b*, *b*), and covered with a plexus of smaller vessels (*c*, *c*).

[1] Various methods of preparing the animal for examination have been employed. The one we have found most convenient, in examining the circulation in the frog, is to break up the medulla with a needle, an operation which

In vessels of considerable size, as well as in some capillaries, the corpuscles, occupying the central portion, move with much greater rapidity than the rest of the blood, leaving a layer of clear plasma at the sides, which is nearly motionless. This curious phenomenon is in obedience to a physical law regulating the passage of liquids through capillary tubes for which they have an attraction, such as exists, for example, between the blood and the vessels. In tubes reduced to a diameter approximating that of the capillaries, the attractive force exerted by their walls upon a liquid, causing it to enter the tube to a certain distance, called capillary attraction, becomes an obstacle to the passage of fluid in obedience to pressure. Of course, as the diameter of the tube is re-

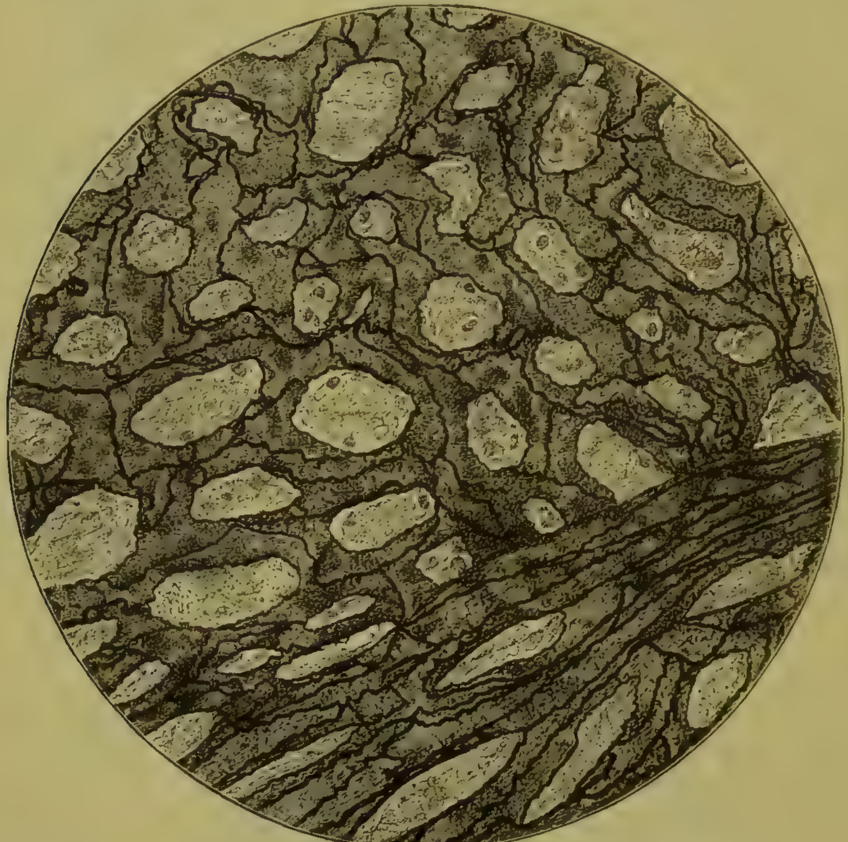


FIG. 31.—*Small artery and capillaries from the lung of a frog; magnified* 500 *diameters.* (From a photograph taken at the United States Army Medical Museum.)

duced, this force becomes relatively increased, for a larger proportion of the liquid contents is brought in contact with it. When we come to the smallest arteries and veins, and still more the capillaries, the capillary attraction is sufficient to produce the motionless layer, called the "still layer" by many physiologists, and the liquid moves only in the central portion. The plasma occupies the position next the walls of the vessels, for it is this portion of the blood which is capable of "wetting" the tubes. The trans-

does not interfere with the circulation, and to attach the animal by pins to a thin piece of cork, stretching the web over an orifice in the cork, to allow the passage of light, and securing it with pins through the toes. The membrane is then moistened with water and covered with thin glass, and, if the general surface be kept moist, the circulation may be studied for hours. By gently inflating the lungs with a small blow-pipe, securing the air by a ligature passed around the larynx beneath the mucous membrane, and opening the chest, the pulmonary circulation may be studied. The circulation may be examined in the tongue (which presents a magnificent view of the circulation as well as of the nerves and muscular fibres) by drawing it out of the mouth and spreading it into a thin sheet, securing it with pins. The circulation may also be observed in the mesentery of a small, warm-blooded animal, like the mouse, by fixing it upon the frog-plate, opening the abdomen, and drawing out the membrane; but it is not seen so well or so conveniently as in the tongue or web of the frog.

parent layer was observed by Malpighi, Haller, and all who have described the capillary circulation. Poiseuille recognized its true relation to the blood-current and explained the phenomenon of the still layer by physical laws, which had been previously established with regard to the flow of liquids in tubes of the diameter of from one-twenty-fifth to one-eighth of an inch, but which he had succeeded in applying to tubes of the size of the capillaries.

A red corpuscle occasionally becomes involved in the still layer, when it moves slowly, turning over and over, or even remains stationary for a time, until it is taken up again and carried along with the central current. A few white corpuscles are constantly seen in this layer. They move along slowly and apparently have a tendency to adhere to the walls of the vessel. This is due to the adhesive character of the surface of the white corpuscles as compared with the red, which can easily be observed in examining a drop of blood between glass surfaces, the red corpuscles moving about with great facility, while the white have a tendency to adhere.

Great differences exist in the character of the flow of blood in the three varieties of vessels which are under observation. In the arterioles, which may be distinguished from the capillaries by their size and the presence of the muscular and fibrous coats, the movement is distinctly remittent, even in their most minute ramifications. The blood moves in them with much greater rapidity than in either the capillaries or veins. They become smaller as they branch, and carry the blood always in the direction of the capillaries. The veins, which are relatively larger than the arteries, carry the blood more slowly and in a continuous stream from the capillaries toward the heart. In both the arteries and veins, the current is frequently so rapid that the form of the corpuscles cannot be distinguished. Only a portion of the white corpuscles occupy the still layer, the rest being carried on in the central current.

The circulation in the true capillaries is *sui generis*. Here the blood is distributed in every direction, in vessels of nearly uniform diameter. The vessels are generally so small as to admit but a single row of corpuscles, which move almost like beings endowed with volition. In a single vessel, a line of corpuscles may be seen moving in one direction at one moment, a few moments after, taking a directly opposite course. Spallanzani, in one of his observations, describes the following phenomenon: Two single rows of corpuscles, passing in two capillary vessels of equal size, were directed toward a third capillary vessel, formed by the union of the two others, which would itself admit but a single corpuscle. The corpuscles in one of these vessels seemed to hold back until those from the other had passed in, when they followed in their turn. When the circulation is normal, the movement in the capillaries is always quite slow as compared with the movement in the arterioles, and is continuous. Here, at last, the intermittent impulse of the heart is lost. The corpuscles do not necessarily circulate in all the capillaries which are in the field of view. Certain vessels may not receive a corpuscle for some time, but, after a while, one or two corpuscles become engaged in them and a current is finally established.

Many interesting little points may be noticed in examining the circulation for a sufficient length of time. A corpuscle is frequently seen caught at the angle where a vessel divides into two, remaining fixed for a time, distorted and bent by the force of the current. It soon becomes released, and, as it enters the vessel, it regains its original form. In some of the vessels of smallest size, the corpuscles are slightly deformed as they pass through. The scene is changed with every different part which is examined. In the tongue, in addition to the arterioles and venules with the rich net-work of capillaries, dark-bordered nerve-fibres, striated muscular fibres, and pavement-epithelium can be distinguished. In the lungs, the view is very beautiful. Large, polygonal air-cells are observed, bounded by capillary vessels, in which the corpuscles move with extreme rapidity. It has been observed that the larger vessels are crowded to their utmost capacity with corpuscles, leaving no still layer next the walls, such as is seen in the circulation in other situations.

When the circulation has been for a long time under observation, as the animal becomes enfeebled, very interesting changes in the character of the flow of blood take place. The continuous stream in the smallest vessels diminishes in rapidity, and, after a time, when the contractions of the heart have become infrequent and feeble, the blood is nearly arrested, even in the smallest capillaries, during the intervals of the heart's action, and the current becomes remittent. As the central organ becomes more and more enfeebled, the circulation becomes intermittent, and the blood receives an impulse from each contraction, remaining stationary during the intervals. At this time, the corpuscles cease to occupy exclusively the central portion of the vessels, and the clear layer

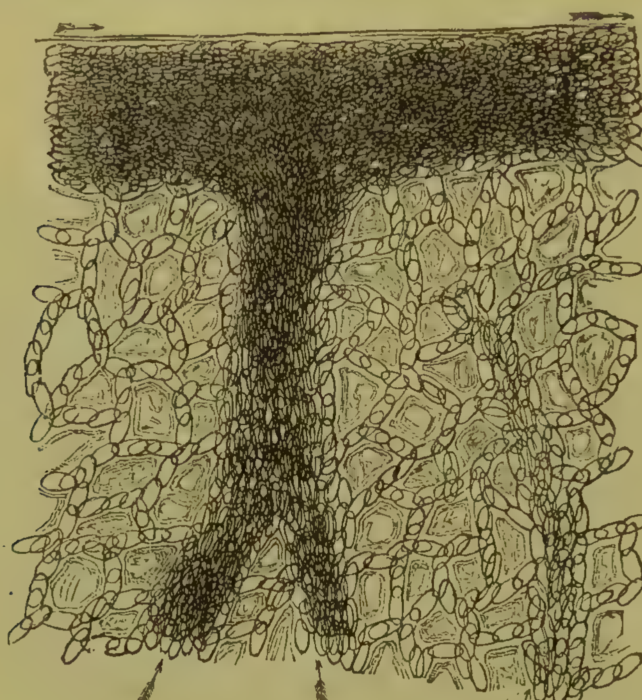


FIG. 32.—*Portion of the lung of a live triton, drawn under the microscope and magnified* 150 *diameters.* (Wagner.)

of plasma next their walls, which was observed in the normal circulation, is no longer apparent. Following this, there is an actual oscillation in the capillaries. At each contraction of the heart, the blood is forced onward a little distance, but it almost immediately returns to about its former position. This phenomenon has long been observed and is explained in the following way: As the heart has become enfeebled, the contractions are so infrequent and ineffectual, that, during their intervals, the constant flow in the capillaries is entirely arrested; for the arterial pressure, which is its immediate cause and which is maintained by the successive charges of blood sent into the arteries at each ventricular systole, is lost. But, as the blood is contained in a connected system of closed tubes, the feeble impulse of the heart is propagated through the vessels and produces a slight impulse, even in the smallest capillaries, which dilates them and forces the fluid a little distance. As soon, however, as the heart ceases to contract, the current is arrested, and the blood, meeting with a certain amount of obstruction from the fluid in the small veins, which are still farther removed from the heart, is made to return to its former position. This phenomenon continues for a short time only, for the heart soon loses its contractility, and the circulation in all the vessels is permanently arrested.

Rapidity of the Capillary Circulation.—The circulation in the capillaries of a part is subject to such great variations, and the differences in different situations are so considerable, that it is impossible to give any definite rate which will represent the general rapidity of the capillary circulation. It is for this reason that it has been found impracticable to estimate the capacity of the capillary as compared with the arterial system. The rapidity of the flow of blood is by no means so great as it appears in microscopical examinations, being, of course, exaggerated in proportion to the magnifying power employed. It is, nevertheless, to microscopical investigations that we are indebted for the scanty information we possess on this subject. The estimates which have been made by various observers refer generally to cold-blooded animals and have been arrived at by simply calculating the time occupied by a blood-corpuscle in passing over a certain distance. Hales, who was the first to investigate this question, estimated that, in the frog, a corpuscle moved at the rate of an inch in ninety seconds. The estimates of Weber and Valentin are considerably higher, being about one-fiftieth of an inch per second. Volkmann calculated the rapidity in the mesentery of the dog, which would approximate more nearly to the human subject, and found it to be about one-thirtieth of an inch per second. Vierordt made a number of curious observations upon himself, by which he professed to be able to estimate the rapidity of the circulation in the little vessels of the eye. He states that when the eye is fatigued, and sometimes when the nervous system is disordered, compression of the globe in a certain way will enable one to see a current like that in a capillary plexus. This he believed to be the capillary circulation, and, by certain calculations, he formed an estimate of its rapidity, putting it at from one-fortieth to one-twenty-eighth of an inch per second. The latter figure accords pretty nearly with the observations of Volkmann upon the dog. How far these observations are to be relied upon, it is impossible to say. Certainly no great importance would be attached to them if they did not, in their results, approximate to the estimates of Volkmann, which probably represent, more nearly than any, the rapidity of the current in the capillaries of the human subject. After what has been said of the variations in the capillary circulation, it is evident that the foregoing estimates are by no means to be considered exact.

Relations of the Capillary Circulation to Respiration.—In treating of the influence of respiration upon the action of the heart, the arterial pressure, pulse, etc., it has already been stated that non-aërated blood cannot circulate freely in the capillaries. Various ideas with regard to the effects of asphyxia upon the circulation have been advanced, which will be again discussed in connection with respiration. The fact is evident that arrest of respiration produces arrest of circulation. This is ordinarily attributed to an impediment to the passage of blood through the lungs when they no longer contain the proper quantity of oxygen. This view is entirely theoretical and has been disproved by experiments dating more than half a century ago. In 1789, Goodwyn advanced the theory that, in asphyxia, the blood passes through the lungs but is incapable of exciting contractions in the left ventricle. Bichat, in his celebrated essay "*Sur la vie et la mort*," 1805, proved by experiment that black blood passes through the lungs in asphyxia and is found in the arteries. His theory was that non-aërated blood, circulating in the capillaries of the nervous centres, arrests their function, thus acting indirectly upon the circulation; and that finally the heart itself is paralyzed by the circulation of black blood in its substance.

The immediate effects of asphyxia upon the circulation are referable to the general capillary system. This fact we demonstrated conclusively by experiments upon the frog, published in 1857. In these experiments, the medulla oblongata was broken up, and the web of the foot was submitted to microscopical examination. This operation does not interfere with the circulation, which may be observed for hours without difficulty. The cutaneous surface was then coated with collodion, care only being taken to avoid the web under observation. The effect on the circulation was immediate. It instantly became less rapid, until, at the expiration of twenty minutes, it had entirely ceased. The entire coating of collodion was then instantly peeled off. Quite a rapid circulation immediately commenced, but it soon began to decline and in twenty minutes had almost ceased. In another observation, the coating of collodion was applied without destroying the medulla. The circulation was affected in the same manner as before and ceased in twenty-five minutes. These experiments, taken in connection with observations on the influence of asphyxia upon the arterial pressure, conclusively show that non-aërated blood cannot circulate freely in the systemic capillaries. Venous blood, however, can be forced through them with a syringe, and, even in asphyxia, it slowly filters through. If air be admitted to the lungs before the heart has lost its contractility, the circulation is restored. No differences in the capillary circulation have been noticed accompanying the ordinary acts of inspiration and expiration.

Causes of the Capillary Circulation.—The contractions of the left ventricle are evidently capable of giving an impulse to the blood in the smallest arterioles; for a marked acceleration of the current accompanying each systole can be distinguished in all but the true capillaries. It has also been shown by experiments after death, that blood can be forced through the capillary system and returned by the veins by a force less than that exerted by the left ventricle. This, however, cannot rigidly be applied to the natural circulation, as the smallest arteries are endowed during life with contractility, which is capable of modifying the blood-current. Dr. Sharpey adapted a syringe, with a hæma-dynamometer attached, to the aorta of a dog just killed, and found that fresh defibrinated blood could be made to pass through the double capillary systems of the intestines and liver, by a pressure of three and a half inches of mercury. It spurted out at the vein in a full jet under a pressure of five inches. In this observation, the aorta was tied just above the renal arteries. The same pressure, the ligature being removed, forced the blood through the capillaries of the inferior extremities. This is much less than the arterial pressure, which is equal to from five and a half to six inches of mercury.

It is thus seen that the pressure in the arteries which forces the blood toward the capillaries is competent, unless opposed by excessive contraction of the arterioles, not only to cause the blood to circulate in these vessels, but to return it to the heart by the veins. This fact is so evident, that it is unnecessary to discuss the views of Bichat and some others, who supposed that the action of the heart had no effect upon the capillary circulation. It must be admitted that this is its prime cause; and the only questions to be considered are, first, whether there be any reason why the force of the heart should not operate on the blood in the capillaries, and second, whether there be any force in these vessels which is superadded to the action of the heart. The first of these questions is answered by microscopical observations on the circulation. A distinct impulse, following each ventricular systole, is observed in the smallest arteries; the blood flows from them directly and freely into the capillaries; and there is not the slightest ground for the supposition that the force is not propagated to this system of vessels.

Various writers have supposed the existence of a "capillary power," which they have regarded as of greater or less importance in producing the capillary circulation. The ideas of some are purely theoretical, but others base their opinion on microscopical observations. These views do not demand extended discussion. There is a force in operation, the action of the heart, which is capable of producing the capillary circulation; and there is nothing in the phenomena of the circulation in these vessels, which is inconsistent with its full operation. Under these circumstances, it is unphilosophical to invoke the aid of the currents produced in capillary tubes in which liquids of different characters are brought in contact, or a "capillary power" dependent upon a so-called vital nutritive attraction between the tissues and the blood, unless we do it on the basis of phenomena observed in the capillaries when the action of the heart is suppressed. When the heart ceases its action, movements in the capillaries are sometimes due to the contractions of the arteries, a property which has already been fully considered. Movements which have been observed in membranes detached from the body are due to the mere emptying of the divided vessels or to simple gravitation. It must be remembered that, in microscopical examinations, the movements observed are immensely exaggerated by the magnifying power, and we receive, at first sight, an erroneous impression of their rapidity. The movements of the blood in detached membranes, due merely to gravitation, have been so satisfactorily explained by the experiments of Poiseuille, that it is deemed unnecessary to refer to the observations of those who have attributed this phenomenon to other causes.

Physiologists who, like Bichat, have been unable to explain the local variations in the capillary circulation without the intervention of a force resident in these vessels or in the surrounding tissues, have not appreciated the action of the arterioles. These little vessels are endowed to an eminent degree with contractility and, by the contractions and relaxations of their muscular walls, they regulate the supply of blood to the capillaries of individual parts. Their action is competent to produce all the variations which are observed in the capillary circulation.

It is evident, then, that the arterial pressure, which is itself derived from the action of the heart, is competent to produce the circulation of the blood, as we observe it, with all its variations, in the capillary vessels; that there is no evidence of the intervention of any other force; but, on the contrary, microscopical observations and experiments on the arteries and veins, thus far, show that there is no other force in operation.

It has been asserted that there is a circulation of the blood in the area vasculosa, the first blood-vessels that are developed, before the heart is formed; but there are no definite and reliable observations which show that there is any regular movement of the blood, which can be likened to the circulation as it is observed after the development of the heart, anterior to the appearance of a contractile central organ. Another example of what is supposed to be circulation without the intervention of the heart is in cases of acardiac fœtuses. Monsters without a heart, which have undergone considerable development and which present systems of arteries, capillaries, and veins, have been described. All of these, however, are accompanied by a twin, in which the development of the circulatory system is quite or nearly perfect.

Influence of Temperature on the Capillary Circulation.—Within moderate limits, a low temperature, induced by local applications, has been found to diminish the quantity of blood sent to the capillaries and retard the circulation, while a high temperature increases the supply of blood and accelerates its current. The mechanism of this is beautifully shown by the experiments of Poiseuille. This observer found that when a piece of ice was applied to the web of a frog's foot, the mesentery of a small warm-blooded animal, or to any part in which the capillary circulation can be observed, the number of corpuscles circulating in the arterioles became very much diminished, "those which carried two or three rows of corpuscles giving passage to but a single row." The circulation in the capillaries first became slower and then entirely ceased in parts. On removing the ice, in a very few minutes the circulation regained its former characters. If, on the other hand, the part be covered with water at 104° Fahr., the rapidity of the current in the capillaries is so much increased that we can hardly distinguish the form of the corpuscles.

Influence of Direct Irritation upon the Capillary Circulation.—Experimental researches on the effects of direct irritation of the capillaries, in parts where the circulation can be observed microscopically, have been quite numerous since Thompson studied the effects of saline solutions on the web of the frog's foot, in 1813. The most noticeable papers on this subject are those of Dr. Wilson Philip and Mr. Wharton Jones. The latter paper, which received the Astley Cooper prize for 1850, is based on very extended and carefully-conducted observations, in which the author, by means of various irritants, succeeded in producing very curious and interesting phenomena, which he regarded as inflammatory. It is not our object to discuss the nature of inflammation or to treat of the changes in the character of the capillary circulation which are supposed to attend this condition, as this subject is entirely pathological; but it must be remembered, in considering the effects of direct irritation on the capillary circulation, that the phenomena thus observed in cold-blooded animals cannot be taken as absolutely representing the characters of inflammation in the human subject. When an irritation is applied to a transparent part, the phenomena observed may be due to many causes, as the direct effects upon the contractile elements of the blood-vessels, reflex action through the nervous system, and the direct influence of the application upon the constitution of the blood. Saline or other fluids are competent to modify, to a very considerable extent, the composition of the blood, when separated from it only by the thin, permeable walls of the vessels; and the phenomena which follow their application are necessarily very complex. The process of inflammation is by no means completely understood; but it is pretty generally acknowledged to be a modification of nutrition. We are hardly prepared to admit that this modification, whatever it may be, can be induced under our very eyes, simply by the application of irritants. With these views, microscopical researches on the "state of the blood and blood-vessels in inflammation" do not assume the importance which is attributed to them by many authors. Keeping this in mind, we may state the following as a summary of the phenomena which have been observed in the capillary circulation, as the result of irritation applied to transparent parts:

The application of the irritant is immediately followed by constriction of the arterioles and diminution in the rapidity of the current in them as well as in the capillaries.

This constriction of the vessels is but momentary, if a powerful irritant, like a very strong solution of a salt, be used. It is followed by a dilatation of the vessels and an increase in the rapidity of the circulation.

Soon after the vessels have become dilated, the rapidity of the circulation becomes progressively diminished, until oscillation of the blood in the vessels takes place, which occurs when the circulation is about to cease. This oscillation finally gives place to complete stagnation; and the vessels become crowded with blood, so that the transparent layer next their walls is no longer observed. In this condition, it has often been noticed that the proportion of colorless corpuscles is increased.

Following the contraction and subsequent dilatation of the vessels, there are stasis and engorgement of the parts which have been exposed to irritation. If the irritation be discontinued, this condition is gradually relieved, and the blood resumes its normal current.

In inflammation, as it is observed in the conjunctiva and in other vascular parts, there unquestionably is congestion of the vessels; but there is no positive evidence of stagnation of blood in the parts as a constant occurrence. The circulation seems, indeed, to be more active than in health. With regard to the microscopical phenomena just mentioned, the contraction of the arterioles is simply the effect of a stimulus upon their muscular coats; and dilatation takes place probably in consequence of the excessive contraction, for it has been shown that this condition of the muscular fibres is pretty constantly followed by unusual relaxation. It has never yet been determined how far the stasis of the blood is due to an osmotic action of solutions employed in the experiments.

Circulation of the Blood in the Veins.—The blood, distributed to the capillaries of all the tissues and organs by the arteries, is collected from these parts in the veins and carried back to the heart. In studying the anatomy of the capillary system or in observing the passage of the blood from the capillaries to larger vessels in parts of the living organism which can be submitted to microscopical examination, it is seen that the capillaries, vessels of nearly uniform diameter and anastomosing in every direction, give origin, so to speak, to a system of vessels, which, by union with others as we follow their course, become larger and larger, and carry the blood away in a uniform current. These are called the venules, or venous radicles. They are the peripheral radicles of the numerous vessels which transport the blood, after it has served the purposes of nutrition or secretion, to the central organ.

The venous system may be considered, in general terms, as divided into two sets of vessels; one, which is deep-seated and situated in proximity to the arteries, and the

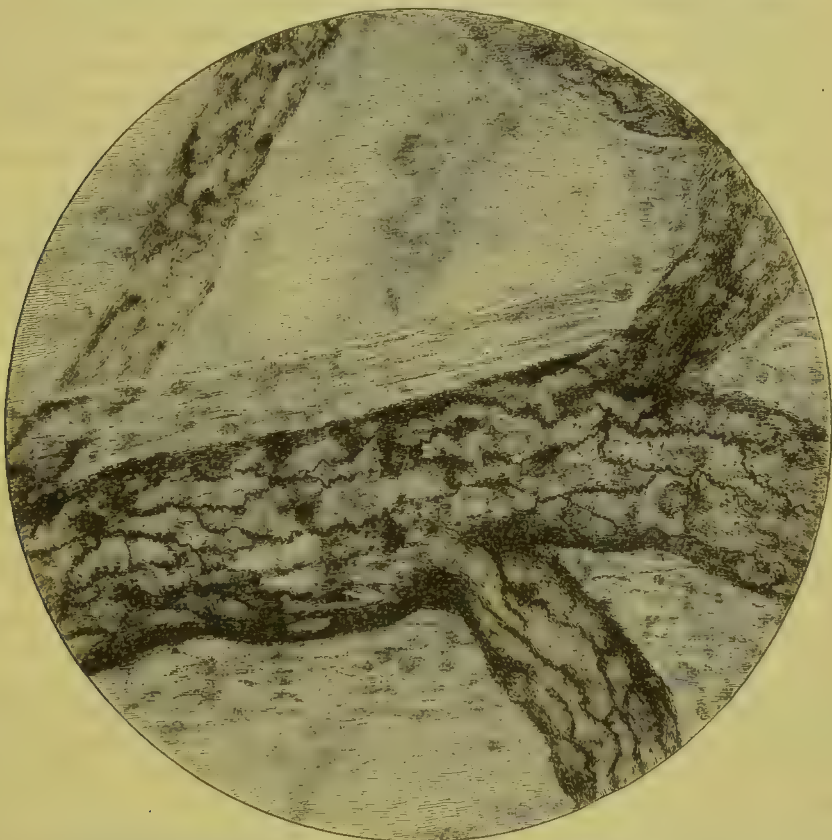


FIG. 33.—*Venous radicles, uniting to form a small vein, from the muscular coat of the urinary bladder of the frog; magnified* 400 *diameters.* (From a photograph taken at the United States Army Medical Museum.) This preparation shows the epithelium of the vessels. It is injected with nitrate of silver, stained with carmine, and mounted in Canada balsam.

other, which is superficial and receives for the most part the blood from the cutaneous surface. The entire capacity of these vessels, as compared with that of the arteries, is very great. As a general rule, each vein, when fully distended, is larger than its adjacent artery. Many arteries are accompanied by two veins, as the arteries of the extremities; while certain of them, like the brachial or spermatic, have more than two. Added to these is the superficial system of veins which have no corresponding arteries. It is true that some arteries have no corresponding veins, but examples of this kind are not sufficiently numerous to diminish, in any marked degree, the great preponderance of the veins, both in number and volume. It is impossible to give an accurate estimate of the extreme capacity of the veins as compared with the arteries; but, from the best information we have, it is several times greater. Borelli estimated that the capacity of the veins was to the capacity of the arteries, as 4 to 1; and Haller, as 2¼ to 1. The proportion is very variable in different parts of the body. In some situations the capacity of the veins and arteries is about equal; while in others, as in the pia mater, the veins will contain, when fully distended, six times as much as the arteries.

In attempting to compare the quantity of blood normally circulating in the veins with that contained in the arteries, we find such variations in the venous system at different times and in different parts, both in the quantity of blood, rapidity of circulation, pressure, etc., that a definite estimate is impossible. It would be unphilosophical to attempt even an approximate comparison, as the variations in the venous circulation constitute one of its greatest and most important physiological peculiarities, which must be fully appreciated in order to form a just idea of the function of the veins. The arteries are always full, and their tension is subject to comparatively slight variations. Following the blood into the capillaries, we observe the immense modifications in the circulation with varying physiological conditions of the parts, to which we have already referred. As would naturally be expected, the condition of the veins varies with the changes in the capillaries, from which the blood is taken. In addition to this, there are independent variations, as in the erectile tissues, in the veins of the alimentary canal during absorption, in veins subject to pressure, etc.

Following the veins in their course, it is observed that anastomoses with each other form the rule, and not the exception as in the arteries. There are always a number of channels by which the blood may be returned from a part; and, if one vessel be obstructed from any cause, the current is simply diverted into another. The veins do not present a true anastomosing plexus, such as exists in the capillary system, but simply an arrangement by which the blood can readily find its way back to the heart, and by which the vessels may accommodate themselves to the immense variations in the quantity of their fluid contents. This, with the peculiar valvular arrangement which exists in all but the veins of the cavities, provides against obstruction to the flow of blood through, as well as from the capillaries, in which it seems essential to the proper nutrition and function of parts that the quantity and course of the blood should be regulated exclusively through the arterial system. Special allusion to the different venous anastomoses belongs to descriptive anatomy. Physiologically, the communications between the different veins are such that the blood can always find a way to the heart, and, once fairly out of the capillaries, it cannot react and influence the circulation of fresh blood in the tissues.

Collected in this way from all parts of the body, the blood is returned to the right auricle, from the head and upper extremities by the superior vena cava, from the trunk and lower extremities, by the inferior vena cava, and from the substance of the heart, by the coronary veins.

Structure and Properties of the Veins.—The structure of the veins is somewhat more complex and difficult of study than that of the arteries. Their walls, which are always much thinner than the walls of the arteries, may be divided into quite a number of layers; but, for convenience of physiological description, we shall regard them as presenting three distinct coats. These have properties which are tolerably distinctive, although not as much so as the three coats of the arteries.

The internal coat of the veins is a continuation of the single coat of the capillaries and of the internal coat of the arteries. It is a simple, homogeneous membrane, somewhat thinner than in the arteries, lined by a delicate layer of polygonal epithelium.

The middle coat is divided by some into two layers; an internal layer, which is composed chiefly of longitudinal fibres, and an external layer, in which the fibres have a circular direction. These two layers are intimately adherent and are quite closely attached to the internal coat. The longitudinal fibres are composed of connective-tissue fibres mingled with a large number of the smallest variety of the elastic fibres. This layer contains a large number of capillary vessels (vasa vasorum). The circular fibres are composed of elastic tissue, some of the fibres of the same variety as is found in the longitudinal layer, some of medium size, and some in the form of the "fenestrated membrane." In addition, there are inelastic fibres interlacing in every direction and mingled with capillary blood-vessels, and the unstriped or involuntary muscular fibres. In the human subject, in the veins of the dura and pia mater, the bones, and the retina, the vena cava descendens, the thoracic portion of the vena cava ascendens, the external and internal jugulars, and the subclavian veins, there are no muscular fibres in the middle coat. In the larger veins, such as the abdominal vena cava, the iliac, crural, popliteal, mesenteric, and axillary veins, the fibres are both circular and transverse. In the smaller veins, the fibres are circular.

The external coat of the veins is composed of white fibrous tissue, like the corresponding coat of the arteries. In the largest veins, particularly those of the abdominal cavity, this coat contains a layer of longitudinal unstriped muscular fibres. In the veins near the heart, are found a few striated fibres, which are continued on to the veins from the auricles. In some of the inferior animals, as the turtle, these fibres are quite thick, and pulsation of the veins in the immediate vicinity of the heart is very marked. In nearly all veins, the external coat is several times thicker than the internal. This is most marked in the larger veins, in which the middle coat, particularly the layer of muscular fibres, is very slightly developed.

In what are called the venous sinuses, and in the veins which pass through bony tissue, we have only the internal coat, to which are superadded a few longitudinal fibres, the whole being closely attached to the surrounding parts. As examples of this, may be mentioned the sinuses of the dura mater and the veins of the large bones of the skull. In the first instance, there is little more than the internal coat of the vein firmly attached to the surrounding layers of the dura mater. In the second instance, the same thin membrane is adherent to canals formed by a layer of compact bony tissue. The veins are much more closely adherent to the surrounding tissues than the arteries, particularly when they pass between layers of aponeurosis.

The above peculiarities in the anatomy of the veins indicate considerable differences in their properties as compared with the arteries. When a vein is cut across, its walls fall together, if not supported by adhesions to surrounding tissues, so that its caliber is nearly or quite obliterated. The yellow elastic tissue, which gives to the larger arteries their great thickness, is very scanty in the veins, and the thin walls collapse when not sustained by liquid in the interior of the vessels. Whenever the veins remain open after section, it is on account of their attachment to surrounding tissues and is not due to the rigidity of the vessels themselves.

Although with much thinner and apparently weaker walls, the veins, as a rule, will resist a greater pressure than the arteries. Observations on the relative strength of the arteries and veins were made by Hales, but the most extended experiments on the subject were made by Clifton Wintringham, in 1740. The latter observer ascertained that the inferior vena cava of a sheep, just above the opening of the renal veins, was ruptured by a pressure of one hundred and seventy-six pounds, while the aorta, at a corresponding point, yielded to a pressure of one hundred and fifty-eight pounds. The strength of the portal vein was even greater, supporting a pressure of nearly five atmospheres, bearing a relation to the vena cava of six to five; yet these vessels had hardly one-fifth the thickness of the arteries. In the lower extremities in the human subject, the veins are much thicker and stronger than in other situations, a provision against the increased pressure to which they are habitually subjected in the upright posture. Wintringham noticed one singular exception to the general rule just given. In the vessels of the glands and of the spleen, the strength of the arteries was much greater than that of the veins. The splenic vein gave way under a pressure of little more than one atmosphere, while the artery supported a pressure of more than six atmospheres.

A little reflection on the influences to which the venous and arterial circulation are subject will enable us to understand the physiological importance of the great difference in the strength of the two varieties of vessels. It is true that in the arterial system the constant pressure is greater than in the veins; but it is nearly the same throughout the arterial system, and the immense extent of the outlet into the capillary system provides against any very great increase in pressure, so long as the blood is in a condition which enables it to pass into the capillaries. The muscular fibres of the left ventricle have but a limited power, and when the pressure in the arteries is so great, as it sometimes is in asphyxia, as to close the aortic valves so firmly that the force of the ventricle will not open them, it cannot be increased. At the same time, it is being gradually relieved by the capillaries, through which the blood slowly filters, even when completely unaërated. With the veins it is different. The blood has a comparatively restricted outlet at the heart and is received by the capillaries from all parts of the system. The vessels are provided with numerous valves, which render a general backward action impossible. Thus, restricted portions of the venous system, from pressure in the vessels, increase of fluid from absorption, accumulation by force of gravity, and other causes, may be subjected to great and sudden variations in pressure. The great strength of these vessels enables them ordinarily to suffer these variations without injury; although varicose veins in various parts present examples of the effects of repeated and continued distention.

The veins possess a considerable degree of elasticity, although this property is not so marked as it is in the arteries. If we include between two ligatures a portion of a vein distended with blood and make a small opening in the vessel, the blood will be ejected with some force, and the vessel becomes very much reduced in caliber.

It has been proven by direct experiment that the veins are endowed with the peculiar contractility characteristic of the action of the unstriped muscular fibres. On the application of galvanic or mechanical excitation, they contract slowly and gradually, the contraction being followed by a correspondingly-gradual relaxation. There is never any rhythmical or peristaltic movement in the veins, sufficient to assist the circulation. The only regular movements which occur are seen in the vessels in immediate proximity to the right auricle, which are provided with a few fibres similar to those which exist in the walls of the heart.

Nerves, chiefly from the sympathetic system, have been demonstrated in the walls of the larger veins but have not been followed out to the smaller ramifications.

Valves of the Veins.—The discovery of the valves of the veins has already been alluded to in connection with the history of the discovery of the circulation. They had undoubtedly been observed in various parts of the venous system, but Fabricius, the greatest anatomist of his day, had the good fortune to demonstrate them to his illustrious pupil, William Harvey, whose immortal discovery indicated their physiological importance. Being ignorant of the observations of his predecessors on this subject, Fabricius announced himself as their discoverer and is generally so regarded. In all parts of the venous system, except, in general terms in the abdominal, thoracic, and cerebral cavities, there exist little membranous, semilunar folds, resembling the aortic and pulmonic valves of the heart. When distended, the convexities of these valves look toward the periphery. In the great majority of instances, the valves exist in pairs, but they are occasionally found in groups of three. They are formed in part of the lining membrane of the veins, with fine fibres of connective tissue. There exists, also, a fibrous ring following the line of attachment of the valvular curtains to the vein, which renders the vessel much stronger and less dilatable here than in the spaces between the valves. The valves are by far the most numerous in the veins of the lower extremities. They are generally situated just below the point where a small vein empties into one of larger size, so that the blood, as it passes in, finds an immediate obstacle to passage in the wrong direction. The situation of the valves may be readily observed in any of the superficial veins. If the flow of blood be obstructed, little knots will be formed in the congested vessels, which indicate the position and action of the valves. The simple experiment of Harvey, already referred to, presents a striking illustration of the action of the valves. When the vein is thus congested and knotted, if the finger be pressed along the vessel in the direc-

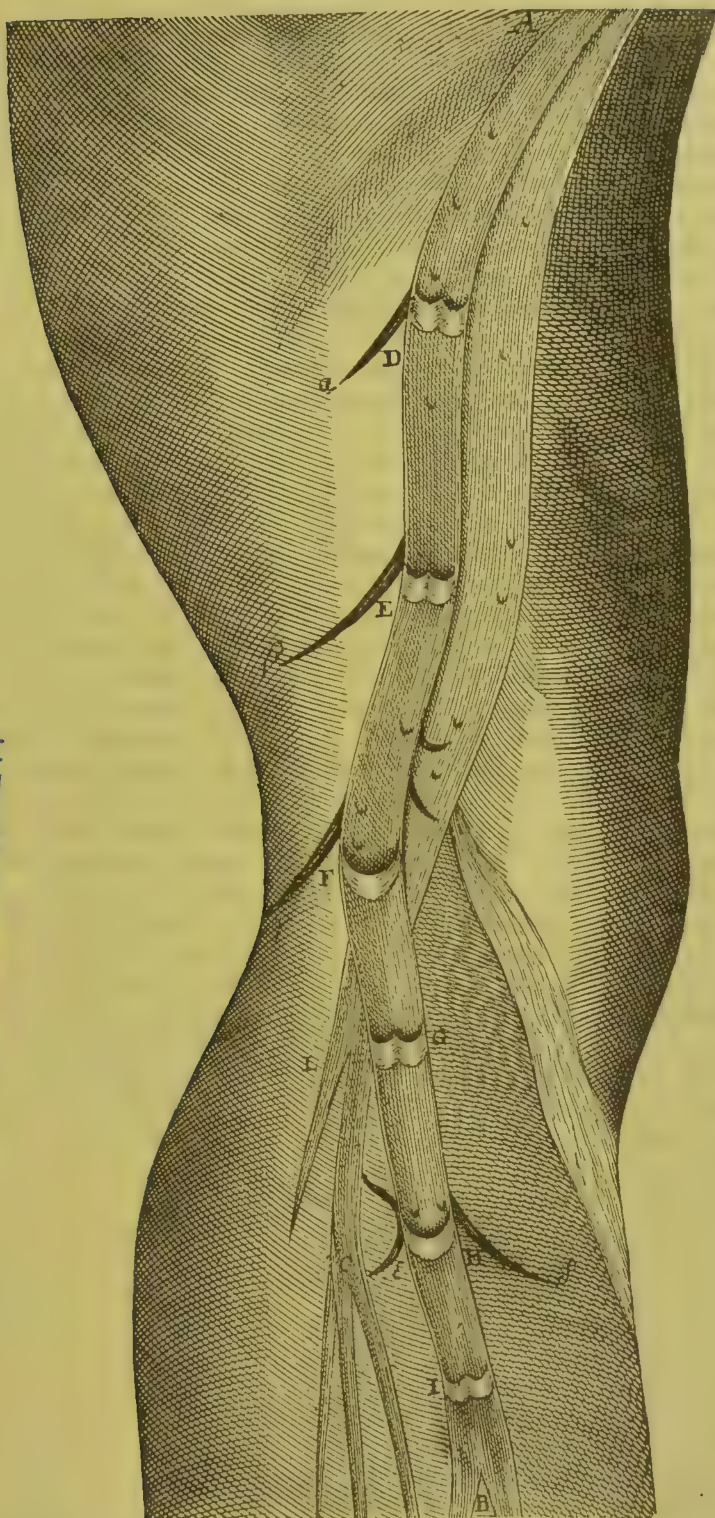


FIG. 34.—*Valves of the veins.* (Copied and reduced from a figure in the original work of Fabricius, published in 1687.) A, B, vein; L, artery; D, E, F, G, H, I, valves; α, β, γ, δ, ϵ, venous branches.

tion of the blood-current, a portion situated between two valves may be emptied of blood; but it is impossible to empty any portion of the vessel by pressing the blood in the opposite direction. On slitting open a vein, we observe the shape, attachment, and extreme delicacy of structure of the valves. When the vessel is empty, or when fluid moves toward the heart, they are closely applied to the walls; but if liquid or air be forced in the opposite direction, they project into its caliber, and, by the application of their free edges to each other, effectually prevent any backward current. Fabricius noted the following peculiarity in the arrangement of the valves: When closed, the application of their free edges forms a line which runs across the vessel; it is found that, in successive sets of valves, these lines are at right angles to each other, so that if, in one set, this line have a direction from before backward, in the sets above and below the lines run from side to side.

There are certain exceptions to the general proposition that the veins of the great cavities are not provided with valves. Valves are found in the portal system of some of the inferior animals, as the horse. They do not exist, however, in this situation in the human subject. Generally, in following out the branches of the inferior vena cava, no valves are found until we come to the crural vein; but occasionally there is a double valve at the origin of the external iliac. In some of the inferior animals, there exists constantly a single valvular fold in the vena cava at the openings of the hepatic, and one at the opening of the renal vein. This is not constant in the human subject. Valves are found in the spermatic, but not in the ovarian veins. A single valvular fold has been described at the opening of the right spermatic into the vena cava. There are two valves in the azygos vein near its opening into the superior vena cava. There is a single valve at the orifice of the coronary vein. There are no valves at the openings of the brachio-cephalic into the superior vena cava; but there is a strong double valve at the point where the internal jugular opens into the brachio-cephalic. Between this point and the capillaries of the brain, the vessels are entirely deprived of valves, except in very rare instances, when one or two are found in the course of the jugular.

In addition to the double, or more rarely triple valves which have just been described, there is another variety, found in certain parts, at the point where a tributary vein opens into a main trunk. This consists of a single fold, which is attached to the smaller vessel but projects into the larger. Its action is to prevent regurgitation, by the same mechanism as that by which the ileo-cæcal valve prevents the passage of matters from the large into the small intestine. These valves are much less numerous than the first variety.

The veins form a system which is adapted to the return of blood to the heart in a comparatively slow and unequal current. Distention of certain portions is provided for; and the vessels are so protected with valves, that whatever influences the current must favor its flow in the direction of the heart.

Course of the Blood in the Veins.—The experiments of Hales and Sharpey, showing that defibrinated blood can be made to pass from the arteries into the capillaries and out at the veins by a pressure less than that which exists in the arterial system, and the observations of Magendie upon the circulation in the leg of a living dog, showing that ligation of the artery arrests the flow in the vein, points which have already been fully discussed in treating of the causes of the capillary circulation, have established, beyond question, the fact that the force exerted by the left ventricle is sufficient to account for the venous circulation. The heart must be regarded as the prime cause of all movement in these vessels. Regarding this as definitely ascertained, there remain to consider, in the study of the course of the blood in the veins, the character of the current, the influence of the vessels themselves, the question of the existence of forces which may assist the *vis a tergo* from the heart, and circumstances which may interfere with the flow of blood.

As a rule, in the normal circulation, the flow of blood in the veins is continuous. The intermittent impulse of the heart, which progressively diminishes as we recede from this organ but is still felt even in the smallest arteries, is lost, as we have seen, in the capillaries. Here, for the first time, the blood moves in a constant current; and, as the pressure in the arteries is continually supplying fresh blood, that which has circulated in the capillaries is forced into the venous radicles in a steady stream. As the supply to the capillaries of different parts is regulated by the action of the small arteries, and as this supply is subject to great variations, there must necessarily be corresponding variations in the current in the veins and in the quantity of blood which these vessels receive. As we should anticipate, then, the venous circulation is subject to very great variations arising from irregularity in the supply of blood, aside from any action of the vessels themselves or any external disturbing influences. Great variations in the venous current are observed in the veins which collect the blood from the intestinal canal. During the intervals of digestion, these vessels carry a comparatively small quantity of blood; but, during digestion, they are laden with the fluids received by absorption, and the quantity is largely increased.

It often happens that a vein becomes obstructed from some cause which is entirely physiological, as the action of muscles. The immense number of veins, as compared with the arteries, and their free communications with each other, provide that the current, under these circumstances, is simply diverted, passing to the heart by another channel. When any part of the venous system is distended, the vessels react on the blood and exert a certain influence on the current, always pressing it toward the heart, for the valves oppose a flow in the opposite direction.

The intermittent action of the heart, which pervades the whole arterial system, is generally absorbed, as it were, in the passage of the blood through the capillaries; but, when the arterioles of any part are very much relaxed, the impulse of the central organ may extend to the veins. Bernard has shown this in the most striking manner, in his well-known experiments on the circulation in the glands. When the glands are pouring out their secretions, the quantity of blood which they receive is very much increased. It is then furnished to supply material for the secretion, and not exclusively for nutrition. If the vein be opened at such a time, it is found that the blood has not lost its arterial character, that the quantity which escapes is increased, and that the flow is in an intermittent jet, as from a divided artery. This is due to the relaxed condition of the arterioles of the part, and the phenomenon thus observed constitutes the true venous pulse. What thus occurs in a restricted portion of the circulatory system may take place in all the veins, though in a less marked degree. Physicians have frequently noticed, after the blood has been flowing for some time in the operation of venesection, that the color changes from black to red, and the stream becomes intermittent, often leading the operator to fear that he has pricked the artery. In all probability, this is due to the relaxation of the arterioles as one of the effects of abstraction of blood, producing the same condition that has been noted in some of the glands during their functional activity. The hypothesis that it is due to an impulse from the adjacent artery is not admissible. Except in the veins near the heart, any pulsation which occurs is to be attributed to the force of the heart, transmitted with unusual facility through the capillary system. A nearly uniform current, however, is the rule, and a marked pulsation, the rare exception.

Pressure of Blood in the Veins.—The pressure in the veins is always much less than in the arteries. It is exceedingly variable in different parts of the venous system and in the same part at different times. As a rule, it is in inverse ratio to the arterial pressure. Whatever favors the passage of blood from the arteries into the capillaries has a tendency to diminish the arterial pressure, and, as it increases the quantity of blood which passes into the veins, must increase the venous pressure. The great capacity of the venous system, its numerous anastomoses, the presence of valves which may shut off a portion from the rest, are circumstances which involve great variations in pressure in different vessels. It has been ascertained that, as a rule, the pressure is diminished as we pass from the periphery toward the heart. In an observation on the calf, Volkmann found that, with a pressure of about 6·5 inches of mercury in the carotid, the pressure in the metatarsal vein was 1·1 inch, and but 0·36 in the jugular. Muscular effort has a marked influence on the force of the circulation in certain veins and produces an elevation in the pressure. As the reduced pressure in the veins is due, in a measure, to the great relative capacity of the venous system and the free communications between the vessels, it would seem that, if it were possible to reduce the capacity of the veins in a part and force all the blood to pass to the heart by a single vessel corresponding to the artery, the pressure in this vessel would be greatly increased. Poiseuille has shown this to be the fact by the experiment of ligating all the veins coming from a part, except one which had the volume of the artery by which the blood was supplied, forcing all the blood to return by this single channel. This being done, he found the pressure in the vein immensely increased, becoming nearly equal to that in the artery.

Rapidity of the Venous Circulation.—It is impossible to fix upon any definite rate as representing the rapidity of the current of blood in the veins. It will be seen that various circumstances are capable of increasing very considerably the rapidity of the flow in certain veins, and that, under certain conditions, the current in some parts of the venous system is very much retarded. Undoubtedly, the general movement of blood in the veins is very much slower than in the arteries, from the fact that the quantity of blood is greater. If it be assumed that the quantity of blood in the veins is double that contained in the arteries, the general average of the current would be diminished one-half. As we near the heart, however, the flow becomes more uniform and progressively increases in rapidity.

As the effect of the heart's action upon the venous circulation is subject to so many modifying influences through the small arteries and capillaries, and as there are other forces influencing the current, which are by no means uniform in their action, with our present knowledge, estimates of the general rapidity of the venous circulation or the variations in different vessels would be founded on mere speculations.

Causes of the Venous Circulation.

In the veins, the blood is farthest removed from the influence of the contractions of the left ventricle; and, although these are felt, there are many other causes which combine to carry on the circulation, and many influences by which it is retarded or obstructed.

The great and uniform force which operates on the circulation in these vessels is the *vis a tergo*. We have repeatedly referred to the entire adequacy of the arterial pressure, propagated through the capillaries, to account for the movement of blood in the veins, provided there be no great obstacles to the current. There are no facts which lead us to doubt the operation of this force as the prime cause of the venous circulation; and the only question which arises is whether there be any force exerted in the capillaries themselves which is superadded to the force of the heart. In discussing the capillary circulation, we stated that there is no direct proof of the existence of a distinct "capillary power" influencing the movement of blood in these vessels; and consequently the *vis a tergo* operating on the circulation in the veins must be attributed mainly to the action of the left ventricle.

The other forces which concur to produce movement of blood in the veins are the following:

1. Muscular action, by which many of the veins are at times compressed, thus forcing the blood toward the heart, regurgitation being prevented by the action of the valves.

2. A suction force exerted by the action of the thorax in respiration, operating, however, only on the veins in the immediate neighborhood of the chest.

3. A possible influence from contraction of the coats of the vessels themselves. This is marked in the veins near the heart in some of the inferior animals.

4. The force of gravity, which operates only on vessels which carry blood from above downward to the heart, and a slight suction force which may be exerted upon the blood in a small vein as it passes into a larger vessel in which the current is more rapid.

The obstacles to the venous circulation are: Pressure sufficient to obliterate the caliber of a vessel, when, from the free communications with other vessels, the current is simply diverted into another channel; the expulsive efforts of respiration; the contractions of the right side of the heart; and the force of gravity, which operates, in the erect posture, on the current in all excepting the veins of the head, neck, and in parts of the trunk above the heart.

Influence of Muscular Contraction.—That the action of muscles has considerable influence on the current of blood in the veins situated between them and in their substance, has long been recognized. It is exemplified in the operation of venesection, when it is well known that the jet from the vein may be very much increased in force by contraction of the muscles below the opening. This action is so marked, that the parts of the venous system which are situated in the substance of muscles have been compared by Chassaignac to a sponge full of liquid, vigorously pressed by the hand. It must always be remembered, however, that, although the muscles are capable of acting on the blood contained in veins in their substance with great vigor, the heart is fully competent to carry on the venous circulation without their aid; a fact which is exemplified in a striking manner in the venous circulation in paralyzed parts.

It has been shown by actual observations with the hæmadynamometer, that muscular action is capable of immensely increasing the pressure in certain veins. The first definite experiments on this subject were made by Magendie, who showed a pressure of over two inches of mercury produced by a general muscular contraction, on the passage of a galvanic current from a needle plunged into the cervical region of the spinal marrow to one fixed in the muscles of the thigh. The experiments of Bernard have shown this more accurately. This physiologist found that the pressure in the jugular of a horse, in repose, was 1·4 inch; but the action of the muscles in raising the head increased it to a little more than five inches, or nearly four times. These observations show at once the great variations in the current and the important influence of muscular contraction on the venous circulation.

In order that contractions of muscles shall assist the venous circulation, two things are necessary:

1. The contraction must be intermittent. This is always the case in the voluntary muscles. It is a view entertained by many that each muscular fibre relaxes immediately after its contraction, which is instantaneous, and that a certain period of repose is necessary before it can contract again. However this may be, it is well known that all active muscular contraction, as distinguished from the efforts necessary to maintain the body in certain ordinary positions, is intermittent and not very prolonged. Thus the veins, which are partly emptied by the compression, are filled again during the repose of the muscle.

2. There should be no possibility of a retrograde movement of the blood. This condition is fulfilled by the action of the valves. Anatomical researches have shown that these valves are most abundant in veins situated in the substance of or between the muscles, and that they do not exist in the veins of the cavities, which are not subject to the same kind of compression. It is thus that the blood is prevented from passing backward toward the capillary system; and, when the caliber of a vein is reduced by compression, part of its contents must be forced toward the heart. This action of the valves constitutes their most important function.

Milne-Edwards alludes to an important physiological bearing of the acceleration of the venous circulation by contractions of muscles on their nutrition. It is apparently necessary that the supply of blood should be increased in a muscle, in proportion to and during its activity; for at that time its disassimilation is undoubtedly augmented, and there is an increased demand on the blood to supply the waste. It is apparently a provision of Nature that the activity of a muscle, facilitating the passage of blood in its veins and consequently its flow from the capillaries, induces an increased supply of the nutrient fluid. As the development of tissues is generally in proportion to their vascularity, this may account for the increase in the development of muscles which is the almost invariable result of exercise.

Force of Aspiration from the Thorax.—During the act of inspiration, the enlargement of the thorax, by depression of the diaphragm and elevation of the ribs, affects the movements of fluids in all the tubes in its vicinity. The air rushes in by the trachea and expands the lungs, so that they follow the movements of the thoracic walls. The flow of blood into the great arteries is somewhat retarded, as is indicated by a diminution in the arterial pressure; and, finally, the blood in the great veins passes to the heart with greater facility and in increased quantity. This last-mentioned phenomenon can be readily observed, when the veins are prominent, in profound or violent inspiration. The veins at the lower part of the neck are then seen to empty themselves of blood during inspiration, and they become distended during expiration, producing a sort of pulsation which is synchronous with respiration. This can always be observed after exposure of the jugular in the lower part of the neck in an inferior animal. After this operation, if we cause the animal to make violent respiratory efforts, the vein will be almost emptied and collapsed with inspiration and turgid with expiration. The movements of the veins near the thorax have long been observed and have been described with tolerable accuracy. Direct observations on the jugulars show conclusively that the influence of inspiration cannot be felt much beyond these vessels. They are seen to collapse with each inspiratory act, a condition which limits this influence to the veins near the heart. The flaccidity of the walls of the veins will not permit the extended action of any suction force. If a portion of a vein removed from the body be attached to the nozzle of a syringe and we attempt to draw a liquid through it, although the suction force be applied very gently, when the vessel has any considerable length its walls will be drawn together. In the circulation, the veins are moderately distended with blood by the *vis a tergo*, and, to a certain extent, they are supported by connections with surrounding tissues, so that the force of aspiration is felt farther than in any experiment on vessels removed from the body. The blood, as it approaches the thorax, impelled by other forces, is considerably accelerated in its flow; but it is seen by direct observation, that beyond a certain point, and that very near the chest, ordinary aspiration has no influence, and violent efforts rather retard than favor the venous current.

In the liver, the influence of inspiration becomes a very important element in the mechanism of the circulation. This organ presents a vascular arrangement which is exceptional. The blood, distributed by the arteries in a capillary plexus in the mucous membrane of the alimentary canal and in the spleen, instead of being returned directly to the heart by the veins, is collected into the portal vein, carried to the liver, and is there distributed in a second set of capillary vessels. It is then collected in the hepatic veins and carried by the vena cava to the heart. This double capillary plexus between the left and the right side of the heart has been cited as an argument against the fact that the left ventricle is capable of sending the blood through the entire circuit of the vascular system. The three hepatic veins open into the inferior vena cava near the point where it passes the diaphragm, where the force of aspiration from the thorax would materially assist the current of blood. On following these vessels into the substance of the liver, it is found that their walls are so firmly adherent to the tissue of the organ, that, when cut across, they remain patulous; and it is evident that they remain open under all conditions. The thorax can therefore exert a powerful influence upon the hepatic circulation; for it is only the flaccidity of the walls of the vessels which prevents this influence from operating throughout the entire venous system. Although this must be a very important element in the production of the circulation in the liver, the fact that the blood circulates in this organ in the fœtus before any movements of the thorax take place shows that it is not absolutely essential. All the influences which we have thus far considered are merely supplementary to the action of the great central organ of the circulation.

A farther proof, if any were needed, of the suction force of inspiration is found in an accident which is not infrequent in surgical operations in the lower part of the neck. When the veins in this situation are kept open by a tumor or by induration of the surrounding tissues, an inspiratory effort has occasionally been followed by the entrance of air into the circulation, an accident which is liable to lead to the gravest results. This occurs only when a divided vein is kept patulous; and the accident proves both the influence of inspiration on liquids in the veins near the chest and its restriction to the vessels in this particular situation by the flaccidity of their walls.

A full discussion of the subject of air in the veins, which is of great pathological interest, does not belong to physiology. The blood is capable of dissolving a certain quantity of atmospheric air; and a small quantity, very gradually introduced into a vein, can be disposed of in this way. When, however, a considerable quantity suddenly finds its way into the venous system, the patient experiences a sense of mortal distress and almost immediately falls into a state of insensibility. A peculiar whistling sound is heard when the air passes in; and, if the ear be applied to the chest, we distinguish the labored efforts of the heart, accompanied by a loud churning sound. On opening the chest after death, the right cavities of the heart are invariably found distended with air and blood, the blood being frothy and florid. Generally the left side of the heart is nearly or quite empty.

The production of death from air in the veins is purely mechanical. The air, finding its way to the right ventricle, is mixed with the blood in the form of minute bubbles and is carried into the pulmonary artery. Once in this vessel, it is impossible for it to pass through the capillaries of the lungs, and death by suffocation is the inevitable result, if the quantity of air be large. It is because no blood can pass through the lungs, that the left cavities of the heart are usually found empty.

Air injected into the arteries produces no such serious effects as air in the veins. It is arrested in the capillaries of certain parts and in the course of time is absorbed without producing any injury.

Aside from the pressure exerted by the contraction of muscles and the force of aspiration from the thorax, the influences which assist the venous circulation are very slight. As far as the action of the coats of the vessels themselves is concerned, their contraction, it must be remembered, is slow and gradual, like the contraction of the arteries; and it is hardly possible that, in the general venous system, this should operate at all on the blood-current, beyond the simple influence of the reduction of the caliber of the vessel. There is a slight contraction in the venæ cavæ in the immediate proximity of the heart, which is very much more extended in many of the lower vertebrate animals and may be mentioned as having an influence, very insignificant it is true, on the flow of blood from the great veins.

In the veins which pass from above downward, the force of gravity favors the flow of blood. This is seen by the turgescence of the veins of the neck and face, when the head is kept for a short time below the level of the heart. If the arm be elevated above the head, the veins of the back of the hand will be much reduced in size, from the greater facility with which the blood passes to the heart, while they are distended when the hand is allowed to hang by the side and the blood has to mount up against the force of gravity.

In the extreme irregularity in the rapidity of the circulation in different veins, it must frequently happen that a vessel empties its blood into another of larger size, in which the current is more rapid. In such an instance, as a physical necessity, the more rapid current in the larger vessel exerts a certain suction force on the fluid in the vessel which joins with it.

Function of the Valves of the Veins.

It is difficult to comprehend, at the present day, how any anatomist could have accurately described the valves of the veins and yet have been ignorant of their function; and the fact that their use was not understood before the description of the circulation by Harvey shows the greatness of this as a discovery and the shallow character of any pretence that men of science had any definite idea of the motion of the blood before his time.

With our present knowledge of the course of the blood, it is evident that the great function of the valves is to present an obstacle to the reflux of blood toward the capillary system; and it only remains to study the conditions under which they are brought into action.

There are two distinct conditions under which the valves of the veins may be closed. One of them is the arrest of circulation, from any cause, in veins in which the blood has to mount against the force of gravity; and the other, compression of veins, from any cause (generally from muscular contraction) which tends to force the blood from the vessels compressed into others, when the valves offer an obstruction to a flow toward the capillaries and necessitate a current in the direction of the heart. In the first of these conditions, the valves are antagonistic to the force of gravity, and, when the caliber of any vessel is temporarily obliterated, they aid in directing the current into anastomotic vessels. It is but rarely, however, that they act thus in opposition to the force of gravity; and it is only when many of the veins of a part are simultaneously compressed that they aid in diverting the current. When a single vein is obstructed, it is not probable that the valves are necessary to divert the current into other vessels, for this would take place in obedience to the *vis a tergo;* but when many veins are obstructed in a dependent part, and the avenues to the heart become insufficient, the numerous valves divide the columns of blood, so that the pressure is equally distributed throughout the extent of the vessels. For, it must be remembered, the strength of the walls diminishes as we pass from the larger veins to the periphery, and the smallest vessels, which, were it not for the valves, would be subjected to the greatest amount of pressure, are least calculated to bear distention. This is but an occasional function which the valves are called upon to perform; and it is evident that their influence is only to prevent the weight of the entire column of blood, in vessels thus obstructed, from operating on the smallest veins and the capillaries. It cannot make the labor of the heart, when the blood is again put in motion, any less than if the column were undivided, as this organ must have sufficient power to open successively each set of valves, when, of course, they cease to have any influence whatsoever.

It is in connection with the intermittent compression of the veins that the valves have their principal and almost-constant function. Their situation alone would lead to this supposition. They are found in greatest numbers throughout the muscular system, having been demonstrated by Sappey in the smallest venules; they are also found in the upper parts of the body, where they certainly do not operate against the force of gravity; while they do not exist in the cavities, where the venous trunks are not subject to compression. It has already been made sufficiently evident that the action of muscles seconds most powerfully the contractions of the heart. The *vis a tergo* from the heart is, doubtless, generally sufficient to turn this influence of muscular compression from the capillary system, and the valves of the veins are open; but they stand ready, nevertheless, to oppose any tendency to regurgitation.

In the action of muscles, the skin is frequently stretched over the part, and the cutaneous veins are somewhat compressed. This may be seen in the hand, by letting it hang by the side until the veins become somewhat swollen, and then contracting the muscles, when the skin will become tense and the veins are very much less prominent. Here the valves have an important action. The compression of the veins is much greater in the substance of and between the muscles than in the skin; but the blood is forced from the muscles into the skin, and the valves act to prevent it from taking a retrograde course. The fact that the contraction of muscles forces blood into the veins of the skin may be seen by surrounding the upper part of the forearm with a moderately-tight ligature, which will distend the cutaneous veins below. If we now contract the muscles vigorously, the veins below will become sensibly more distended and knotted; showing, at once, the passage of blood into the skin and the action of the valves.

When a vein is distended by the injection of air or a liquid forced against the valves, it is observed that, at the point where the convex borders of the valves are attached, the vessel is not dilated as much as at other parts. This is due to the fact that the valves are bordered with a fibrous ring which strengthens the vessel and prevents distention at that point, which would otherwise separate the free borders of the valves and render them insufficient.

A full consideration of the venous anastomoses belongs to descriptive anatomy. Suffice it to say, in this connection, that they are very numerous and provide for a return of the blood to the heart by a number of channels. The azygos vein, the veins of the spinal canal, and veins in the walls of the abdomen and thorax, connect the inferior with the superior vena cava. Even the portal vein has lately been shown to have its communications with the general venous system. Thus, in all parts of the organism, temporary compression of a vein only diverts the current into some other vessel, and permanent obliteration of a vein produces enlargement of communicating branches, which soon become sufficient to meet all the requirements of the circulation.

Conditions which impede the Venous Circulation.

Influence of Expiration.—The influence of expiration on the circulation in the veins near the thorax is directly opposed to that of inspiration. As the act of inspiration has a tendency to draw the blood from these vessels into the chest, the act of expiration assists in forcing the blood out from the vessels of the thorax and opposes a flow in the opposite direction. The effect of prolonged and violent expiratory efforts is very marked, being followed by deep congestion of the veins of the face and neck and a sense of fulness in the head, which may become very distressing. The opposition to the venous current generally extends only to vessels in the immediate vicinity of the thorax, or, it may be stated in general terms, to those veins in which the flow of blood is assisted by the movements of inspiration; but, while the inspiratory influence is absolutely confined to a very restricted circuit of vessels, the obstructive influence of very violent and prolonged expiration may be extended very much farther, as is seen when the vessels of the neck, face, and conjunctiva become congested in prolonged vocal efforts, blowing, etc. The mechanism of this is not what we might at first be led to suppose; namely, a mere reflux from the large trunks of the thoracic cavity. Were this the case, it would be necessary to assume an insufficiency of certain valves, which does not exist. In extreme congestion, reflux of blood may take place to a certain extent in the external jugular, for this vessel has but two valves, which are not competent to prevent regurgitation; the chief cause of congestion, however, is due, not to regurgitation, but to accumulation from the periphery and an obstruction to the flow of blood into the great vessels.

It is in the internal jugular that the influence of expiration is most important, both from its great size in the human subject, as compared with the other vessels, and from the importance and delicacy of the parts from which it collects the blood. At the opening of this vessel into the innominate vein, is a pair of strong and perfect valves, which effectually close the orifice when there is a tendency to regurgitation. These valves have attracted much attention among physiologists since the discovery of the circulation has made it evident how important they may be in protecting the brain from reflux of blood. When the act of expiration arrests the onward flow in the veins near the thorax, these valves are closed and effectually protect the brain from congestion by regurgitation. The blood accumulates behind the valves, but the free communication of the internal jugular with the other veins of the neck relieves the brain from congestion, unless the effort be extraordinarily violent and prolonged.

The above remarks with regard to the influence of expiration are applicable to vocal efforts, violent coughing or sneezing, or any unusual muscular efforts, such as straining, in which the glottis is closed.

Regurgitant Venous Pulse.—In the inferior animals, like the dog, if the external jugular be exposed, a distention of the vessel is seen to accompany each expiratory act. This is sometimes observed in the human subject, when respiration is exaggerated, and has been called improperly the venous pulse. There is no sufficient obstacle to the regurgitation of blood from the thorax into the external jugular, and distinct pulsations, synchronous with the movements of respiration, may be produced in this way.

It is evident that there are various other circumstances which may impede the venous circulation. Accidental compression may temporarily arrest the flow in any particular vein. When the whole volume of blood is materially increased, as after a full meal with copious ingestion of liquids, the additional quantity of blood accumulates chiefly in the venous system and proportionately diminishes the rapidity of the venous circulation.

The force of gravity also has an important influence. It is much more difficult for the blood to mount from below upward to the heart than to flow downward from the head and neck. The action of this is seen if comparison be made between the circulation in the arm elevated above the head and hanging by the side. In the one case the veins are readily emptied and contain but little blood, and in the other the circulation is more difficult and the vessels are moderately distended. The walls of the veins are thickest and the valves are most numerous in parts of the body which are habitually dependent. The influence of gravity is exemplified in the production of varicose veins in the lower extremities. This disease is frequently induced by occupations which require constant standing; but the exercise of walking, aiding the venous circulation, as it does, by the muscular effort, has no such tendency.

Circulation in the Cranial Cavity.—In the encephalic cavity, there are certain peculiarities in the anatomy of some of the vessels, with exceptional conditions of the blood as regards atmospheric pressure, which have been considered capable of essentially modifying the circulation. In the adult, the cranium is a closed, air-tight box, containing the incompressible cerebral substance, and blood; conditions which are widely different from those presented in other parts of the system. On this account some have gone so far as to consider that any change in the quantity of circulating fluid in the brain is a physical impossibility. Pathological facts in opposition to such a view are so numerous and well established that the question does not now demand extended discussion; but it is nevertheless true that there are anatomical peculiarities in these parts, the effects of which on the circulation present important and interesting points for study.

In the brain, the venous passages which correspond to the great veins of other parts are in the form of sinuses between the folds of the dura mater and are but slightly dilatable. In the perfectly-consolidated adult head, the blood is not subjected to atmospheric pressure, as in other parts, and the semisolids and liquids which compose the encephalic mass cannot increase in size in congestion and diminish in anæmia. Notwithstanding these conditions, the fact remains, that examinations of the vessels of the brain after death show great differences in the quantity of blood which they contain. The question then arises as to what is displaced to make room for the blood in congestion, and what supplies the place of the blood in anæmia. An anatomical peculiarity, which has not yet been considered, offers an explanation of these phenomena. Magendie has shown, by observations on living animals, confirmed by dissections of the human body, that between the pia mater and the arachnoid of the brain and spinal cord there exists a liquid, the cephalo-rachidian fluid, which is capable of passing from the surface of the brain to the spinal canal and communicates with the fluid in the ventricles. This he has conclusively demonstrated to be situated, not between the layers of the arachnoid, as was supposed by Bichat, but between the inner layer of this membrane and the pia mater. The communication between the cranial cavity and the spinal canal is very free. This has been demonstrated by exposing the dura mater of the brain and of the cord, making an opening in the membranes of the cord so as to allow the liquid to escape (which it does in quite a forcible jet), when pressure on the membranes of the brain not only accelerated the flow but pressed out a quantity of the liquid after all that would escape spontaneously had been evacuated. It is easy to see one of the physiological uses of this liquid. When the pressure of blood in the arteries leading to the brain is increased or when there is an obstacle to its return by the veins, more or less congestion takes place, and the blood forces the liquid from the cranial into the spinal cavity; the reverse taking place when the supply of blood to the brain is diminished. The functions of all highly-organized and vascular parts seem to require certain variations in the supply of blood; and there is no reason to suppose that the brain, in its varied conditions of activity and repose, is any exception to this general rule, although the physiological conditions of its vascularity are not easily studied.

Physiologists, even before the time of Haller, had noticed alternate movements of expansion and contraction in the brain, connected with the acts of respiration. This is observed in children before the fontanels are closed, and in the adult when the brain is exposed by an injury or a surgical operation. The movements are, an expansion with the act of expiration, which, in violent efforts, is sometimes so considerable as to produce protrusion, and contraction with inspiration. Magendie also studied these movements, which he explained in the following way: With the act of expiration, the flow of blood in the arteries is favored, and the current in the veins is retarded. If the effort be violent, the valve at the opening of the internal jugular may be closed. This act would produce an expansion of the brain, not from reflux by the veins, but from the fact that the flow into the chest is impeded, and the blood, while passing in more freely by the arteries, is momentarily confined. With inspiration, the flow into the thorax is materially aided, and the brain is in some degree relieved of this expanding force.

Robin, His, and others have noted a peculiarity in the small vessels of the brain, spinal cord, and pia mater, which is curious, but the physiological significance of which is not yet apparent. These vessels are surrounded by a thin, amorphous sheath, which has a diameter of from $\frac{1}{1200}$ to $\frac{1}{400}$ of an inch greater than that of the vessel itself. Between this and the blood-vessel is a transparent liquid. This structure, which has been observed in no other part of the circulatory system, is regarded by Robin as the commencement of the lymphatics of the nervous centres. What effect this disposition of the vessels may have upon the facility with which they may become dilated or contracted, it is difficult to determine.

Circulation in Erectile Tissues.—In the organs of generation of both sexes, there exists a tissue which is subject to great increase in volume and rigidity when in a state of what is called erection. The parts in which the erectile tissue exists are, in the male, the corpora cavernosa of the penis, the corpora spongiosa, with the glans penis; and, in the female, the corpora cavernosa of the clitoris, the gland of the clitoris, and the bulb of the vestibule. In addition, Rouget has lately demonstrated the presence of a structure analogous to erectile tissue in the body of the uterus and in a bulb annexed to the ovary of the human female. He has shown by injections that the uterus is capable of erection like the penis. In some other parts, such as the nipple and the mucous membrane of the vagina, which are sometimes described as erectile, the peculiar vascular arrangement which is characteristic of true erectile tissues is not found. In the nipple, the hardness which follows gentle stimulation is simply the result of contraction of the smooth muscular fibres with which this part is largely supplied, and it is analogous to the elevation of the follicles of the skin from the same cause, in what is called goose-flesh. In the vagina, congestion may occur, as in other mucous membranes, but there is no proper erection.

The vascular arrangement in erectile organs, of which the penis may be taken as the type, is peculiar to them and is not found in any other part of the circulatory system. Taking the penis as an example, the arteries, which have an unusually-thick muscular coat, after they have entered the organ, do not simply branch and divide dichotomously, as in most other parts, but send off large numbers of arborescent branches, which immediately become tortuous and are distributed in the cavernous and spongy bodies in numerous anastomosing vessels, with but a single thin, homogeneous coat, like the true capillaries. These vessels are larger, even, than the arterioles which supply them with blood, some having a diameter of from $\frac{1}{25}$ to $\frac{1}{17}$ of an inch. The cavernous bodies have an external investment of strong fibrous tissue of considerable elasticity, which sends bands, or trabeculæ, into the interior, by which it is divided up into cells. The trabeculæ are composed of fibrous tissue mixed with a large number of smooth muscular fibres. These cells lodge the blood-vessels, which ramify in the tortuous manner already indicated and finally terminate in the veins. The anatomy of the corpora spongiosa is essentially the same, the only difference being that the fibrous envelope and the trabeculæ are more delicate and the cells are of smaller size.

Without going fully into the mechanism of erection, which comes more properly under the head of generation, it may be stated in general terms that, during sexual excitement, or when erection occurs from any cause, the thick muscular walls of the arteries of supply relax and allow the arterial pressure to distend the capacious vessels lodged in the cells of the cavernous and spongy bodies. This produces the characteristic change in the volume and position of the organ. It is evident that erection depends upon the peculiar arrangement of the blood-vessels, and is not simply a congestion, such as could occur in any vascular part. During erection, there is not a stasis of blood; but, if it continue for any length of time, the quantity which passes out of the part by the veins must be equal to that which passes in by the arteries.

Derivative Circulation.—In some parts of the circulatory system, there exists a direct communication between the arteries and the veins, so that all the blood does not necessarily pass through the minute vessels which have been described as true capillaries. This peculiarity, which had been noted by Todd and Bowman, Paget, and others, has been closely studied by M. Sucquet, who was first led to investigate the subject by noticing that by injecting a very small quantity of fluid, entirely insufficient to fill all the capillaries of a member, it was returned by certain of the veins. On using a black, solidifiable injection, he found that there were certain parts of the upper and lower extremities and the head which became colored by the injection, while other parts were not penetrated. Following this out by dissection, he showed that, in the upper extremity, the skin of the fingers and part of the palm of the hand and the skin over the olecranon are provided with vessels of considerable size, which allowed the fluid injected by the axillary artery to pass directly into some of the veins, while in other parts the veins were entirely empty. Extending his researches to the lower extremity, he found analogous communications between the vessels in the knee, toes, and parts of the sole of the foot. He also found communications in the nose, cheeks, lips, forehead, and ends of the ears, parts which are particularly liable to changes in color from congestion of vessels.

It is evident that, under certain circumstances, a larger quantity of blood than usual may pass through these parts without necessarily penetrating the true capillaries and thus exerting a modifying influence upon nutrition. The changes which are liable to occur in the quantity of blood, in the force of the heart's action, etc., may thus take place without disturbing the circulation in the capillaries, a provision which the functions of the parts would seem to demand.

Pulmonary Circulation.—The vascular system of the lungs merits the name, which is frequently applied to it, of the lesser circulation. The right side of the heart acts simultaneously with the left, but is entirely distinct from it, and its muscular walls are very much less powerful. The pulmonary artery has thinner and more distensible coats than the aorta and distributes its blood to a single system of capillaries, situated very near the heart. We have seen that the orifice of the pulmonary artery is provided with valves which prevent regurgitation into the ventricle. In the substance of the lungs, the pulmonary artery is broken up into capillaries, most of them just large enough to allow the passage of the blood-corpuscles in a single row. These vessels are provided with a single coat and form a very close net-work surrounding the air-cells. From the capillaries the blood is collected by the pulmonary veins and conveyed to the left auricle. There is no great disparity between the arteries and veins of the pulmonary system as regards capacity. The pulmonary veins in the human subject are not provided with valves.

The blood in its passage through the lungs does not meet with the resistance which is presented in the systemic circulation. This fact we have often noticed in injecting defibrinated blood through the lungs of an animal just killed. We have also observed that an injection passes through the lungs as easily when they are collapsed as when they are inflated. The anatomy of the circulatory system in the lungs and of the right side of the heart shows that the blood must pass through these organs with comparative facility. The power of the right ventricle is evidently less than half that of the left, and the pulmonary artery will sustain a much less pressure than the aorta.

The two sides of the heart act simultaneously; and at the same time that the blood is sent by the left ventricle to the system it is sent by the right ventricle to the lungs. Some physiologists have endeavored to measure the pressure of blood in the pulmonary artery. The only experiments which have not involved opening the thoracic cavity, an operation which must interfere materially with the pressure of blood in the pulmonary artery, as it does with the general arterial pressure, are those of Chauveau and Faivre. These observers measured the pressure by connecting a cardiometer with a trocar introduced into the pulmonary artery of a living horse through one of the intercostal spaces, and found it to be about one-third as great as the pressure in the aorta; an estimate which corresponds pretty nearly with the comparative power of the two ventricles, as deduced from the thickness of their muscular walls.

Anatomy teaches us that the capillaries of the lungs have exceedingly delicate walls; and it is evident that rupture of these vessels from excessive action of the heart would lead to grave results. It has already been noted that on the right side the lungs are protected by an insufficiency of the auriculo-ventricular valves, which does not exist on the left side, allowing a certain degree of regurgitation when the heart is acting with unusual force, and thus relieving, to a certain extent, the pulmonary system. This was pointed out by Mr. King, of London, and is called the safety-valve function of the right ventricle. We have noticed, in the heart of the ox, a similar difference between the aortic and the pulmonic semilunar valves. If these be exposed on both sides by cutting away portions of the ventricles, and if a current of liquid be forced against them through the vessels, the aortic valves will be found to entirely prevent the passage of the liquid, even under very great pressure, while the pulmonic valves permit regurgitation under a comparatively inconsiderable force. A little reflection will make it evident that, when the heart is acting with undue vigor, it is quite as important to relieve the lungs by a certain amount of regurgitation from the pulmonary artery as by insufficiency of the tricuspid valves. This insufficiency is important, both at the auriculo-ventricular and the pulmonic orifices, in protecting the delicate structure of the lungs from the variations in force to which the action of both ventricles is constantly liable.

On microscopical examination of the circulation in the lower animals, as the frog, the movement of blood in the capillaries of the lungs does not present any differences from the capillary circulation in other parts, except that the vessels seem more crowded with corpuscles and there is no "still layer" next their walls.

There are no forces of any importance which are superadded to the action of the right ventricle in the production of the arterial, capillary, or venous circulation in the lungs; but there are certain conditions which may obstruct the flow of blood through these parts. We have already noted the effect of introduction of air into the veins in blocking up the capillaries of the lungs and preventing the passage of blood. It is a view pretty generally entertained that in asphyxia the non-aëration of the blood obstructs the pulmonary circulation. We have already considered this subject rather fully in treating of the general effects of arrest of respiration on the circulation. The celebrated experiments of Bichat demonstrated the passage of black blood through the lungs in asphyxia and its presence in the arterial system. The experiments of Dalton and others have shown that, in this condition, the obstruction to the circulation occurs first in the systemic capillaries, and the distention is propagated backward through the great vessels and the left cavities of the heart to the right side. When the heart is exposed in a living animal and artificial respiration is kept up, temporary arrest of the respiration produces engorgement and labored action of both ventricles. There are no observations which show that increase of pressure in the pulmonary artery is the first and the immediate result of asphyxia. It is true that, after death, the right side of the heart is engorged; but it is well known, from observations after death and experiments on living animals, that the tonic contraction of the arteries is competent to empty the blood into the veins; and the facts just stated regarding the insufficiency of the pulmonic semilunar valves explain how the right side of the heart may become engorged as the result of obstruction to the blood-current in the left side. Established facts seem to show that asphyxia does not primarily affect the pulmonary circulation, but that it is possible for venous blood to pass through the lungs without undergoing arterialization.

Circulation in the Walls of the Heart.—The fact that the contractions of the muscular walls of the heart, by which the blood is discharged from the ventricles into the great arteries, necessarily compress the vessels in the substance of the heart itself would lead us to expect certain peculiarities in the cardiac circulation. This question has been lately studied by Lannelongue, who has arrived at the following results:

During the ventricular systole, which discharges the blood into the aorta, the vessels in the substance of the ventricles are nearly empty, and the vessels in the auricular walls are filled. During the auricular systole, the auricular vessels are empty and the ventricular vessels are filled. We can readily understand this when we reflect that the vessels in the substance of the heart must be compressed when the muscular fibres contract.

General Rapidity of the Circulation.

Several questions of considerable physiological interest arise in connection with the general rapidity of the circulation:

1. It would be interesting to determine, if possible, what length of time is occupied by the blood in its passage through the entire circuit of both the lesser and the greater circulation.

2. What is the time required for the passage of the entire mass of blood through the heart?

3. What influence has the number of pulsations of the heart on the general rapidity of the circulation?

The first of these questions is the one which has been most satisfactorily answered by experiments on living animals. In 1827, Hering, a German physiologist, performed the experiment of injecting into the jugular vein of a living animal a harmless substance, which could be easily recognized by its chemical reactions, and noted the time which elapsed before it could be detected in the blood of the vein of the opposite side. This gave the first correct idea of the rapidity of the circulation; for, although the older physiologists had studied the subject, their estimates were founded on calculations which had no accurate basis and gave very varied results. The experiment of Hering is often roughly performed as a physiological demonstration; and we have thus had frequent occasions to verify, in a general way, its accuracy. If, for example, we expose both jugulars in a dog, inject into one a solution of ferrocyanide of potassium in water, and draw a specimen of blood from the other with as little loss of time as possible, it will be found that, within twenty or thirty seconds after the injection, the salt has had time to pass from the jugular to the right heart, thence to the lungs and left heart, and thence through the capillaries of the head and face back to the jugular on the opposite side. Its presence can be determined by the distinct blue color produced on the addition of the perchloride of iron to the serum, if the specimen be allowed to stand, or a clear extract of the blood may be made by boiling with a little sulphate of soda and filtering, treating the colorless liquid thus obtained with the salt of iron. In making the test of the blood-extract or serum, the addition of a drop of nitric acid before the perchloride of iron is added will render the blue reaction much more prompt and distinct if the ferrocyanide be present.

The experiments of Hering were evidently conducted with great care and accuracy. He drew the blood at intervals of five seconds after the commencement of the injection, and thus, by repeated observations, ascertained pretty nearly the rapidity of a circuit of blood in the animals on which he experimented. Others have taken up these investigations and introduced some modifications in the manipulations. Vierordt collected the blood as it flowed, in little vessels fixed on a disk revolving at a known rate, which gave more exactness to the observations; but this method is essentially the same as that employed by Hering, and the results obtained by these two observers nearly correspond.

The length of time occupied by a portion of blood in making a complete circuit of the vascular system, in the human subject, is only to be deduced from observations on the inferior animals; but, before this application is made, it will be well to examine the objections, if any exist, to the experimental procedure above described.

The only objection which could be made is, that a saline solution, introduced into the torrent of the circulation, would have a tendency to diffuse itself throughout the whole mass of blood, it might be, with considerable rapidity. This objection to the observations of Hering has been made by Matteucci and is considered by him as fatal to their accuracy. It certainly is an element which should be taken into account; but, from the definite data which have been obtained concerning the rapidity of the arterial circulation and the inferences which are unavoidable with regard to the rapidity of the venous circulation, it would seem that the saline solution must be carried on by the mere rapidity of the arterial flow to the capillaries, which are very short, taken up from them, and carried on by the veins, and thus through the entire circuit, before it has had time to diffuse itself to any considerable extent. It is not apparent how this objection can be overcome, for a substance must be used which will mix with the blood, otherwise it could not pass through the capillaries.

There seems no reason why, with the above restrictions, the results obtained by Hering should not be accepted, and their application be made to the human subject.

Hering found that the rapidity of the circulation in different animals was in inverse ratio to their size and in direct ratio to the rapidity of the action of the heart.

The following are the mean results in certain of the domestic animals, taking the course from jugular to jugular, when the blood passes through the lungs and through the capillaries of the face and head:

In the Horse,	the circulation is accomplished in		27·3	seconds.
" Dog,	"	"	15·2	"
" Goat,	"	"	12·8	"
" Rabbit,	"	"	6·9	"

Applying these results to the human subject, taking into account the size of the body and the rapidity of the heart's action, the duration of the circuit from one jugular to the other may be estimated at 21·4 seconds, and the general average through the entire system, at 23 seconds. This is simply approximative; but the results in the inferior animals may be received as very nearly, if not entirely accurate.

Estimates of the time required for the passage of the whole mass of blood through the heart are even less definite than the estimate of the general rapidity of the circulation. To arrive at any satisfactory result, it is necessary to know the entire quantity of blood in the body and the exact quantity which passes through the heart at each pulsation. If we divide the whole mass of blood by the quantity discharged from the heart with each ventricular systole, we ascertain the number of pulsations required for the passage of the whole mass of blood through the heart; and, knowing the number of beats per minute, we can ascertain the length of time thus occupied. The objection to this kind of estimate is the inaccuracy of the data respecting the quantity of blood in the system as well as the quantity which passes through the heart with each pulsation. Nevertheless, an estimate can be made, which, if it be not entirely accurate, cannot be very far from the truth.

The entire quantity of blood, according to estimates which seem to be based on the most reliable data, is about one-eighth the weight of the body, or eighteen pounds, in a man weighing one hundred and forty-four. The quantity discharged at each ventricular systole is estimated by Valentin at five ounces, and by Volkmann, at six ounces. In treating of the capacity of the different cavities of the heart, it has been noted that the left ventricle, when fully distended, contains from five to seven ounces. Assuming that, at each systole, the left ventricle discharges all its blood, except perhaps a few drops, and that this quantity in an ordinary-sized man is five ounces (for in the estimates of Robin and Hiffelsheim, the cavities were fully distended, and contained more than under the ordinary conditions of the circulation), it would require fifty-eight pulsations for the passage through the heart of the entire mass of blood. Assuming the pulsations to be seventy-two per minute, this would occupy about forty-eight seconds.

The almost instantaneous action of certain poisons, which must act through the blood, confirms our ideas with regard to the rapidity of the circulation. The intervals between the introduction of some agents, strychnine for example, into the circulation, and the characteristic effects on the system, have been carefully noted by Blake, whose observations coincide pretty closely in their results with the experiments of Hering.

The relation of the rapidity of the circulation to the frequency of the heart's action is a question of considerable interest, which was not neglected in the experiments of Hering. It is evident that, if the charge of blood sent into the arteries be the same, or nearly the same, under all circumstances, any increase in the number of pulsations of the heart would produce a corresponding acceleration of the general current of blood. But this is a proposition which cannot be taken for granted; and there are many facts which favor a contrary opinion. It may be enunciated as a general rule that when the acts of the heart increase in frequency they diminish in force; which renders it probable that the ventricle is most completely distended and emptied when its action is moderately slow. When, however, the pulse is very much accelerated, the increased number of pulsations of the heart might be sufficient to overbalance the diminished force of each act and would thus actually increase the rapidity of the circulation. Hering has settled these questions experimentally. His observations were made on horses, by increasing the frequency of the pulse, on the one hand, physiologically, by exercise, and on the other hand, pathologically, by inducing inflammatory action. He found, in the first instance, that, in a horse, with the heart beating at the rate of thirty-six per minute, with eight respiratory acts, ferrocyanide of potassium injected into the jugular appeared in the vessel on the opposite side after an interval of from twenty to twenty-five seconds. By exercise, the number of pulsations was raised to one hundred per minute, and the rapidity of the circulation was from fifteen to twenty seconds. The observations were made with an interval of twenty-four hours. The same results were obtained in other experiments. Here there is a considerable increase in the rapidity of the circulation following a physiological increase in the number of beats of the heart; but the value of each beat is materially diminished; otherwise, the rapidity of the current would be increased about three times, as the pulse became three times as frequent. In its tranquil action, with the pulse at thirty-six, the heart contracted thirteen times during one circuit of blood; while it required twenty-nine pulsations to send the blood over the same course, after exercise, with the pulse at one hundred; showing a diminution in the value of the ventricular systole of more than one-half. In animals suffering under inflammatory fever, either spontaneous or produced by irritants, the same observer found a diminution in the rapidity of the circulation, accompanying acceleration of the pulse. In one observation, inflammation was produced in the horse by the injection of ammonia into the pericardium. At the commencement of the experiment, the pulse was from seventy-two to eighty-four per minute, and the duration of the circulation was about twenty-five seconds. The next day, with the pulse at ninety, the circulation was accomplished in from thirty-five to forty seconds; and the day following, with the pulse at one hundred, the rapidity of the circulation was diminished to from forty to forty-five seconds.

If we be justified in applying the above-mentioned observations to the human subject (and there is no reason why this should not be done), it is shown that, when the pulse is accelerated in disease, the value of the contractions of the heart, as represented by the quantity of blood discharged, bears an inverse ratio to their number and is so much diminished as absolutely to produce a current of less rapidity than normal.

With regard to the relations between the rapidity of the heart's action and the general rapidity of the circulation, the following conclusions may be given as the results of experimental inquiry:

1. In physiological increase in the number of beats of the heart, as the result of exercise, for example, the general circulation is somewhat increased in rapidity, though not in proportion to the increase in the pulse.

2. In pathological increase of the heart's action, as in febrile movement, the rapidity of the general circulation is generally diminished, it may be, to a very great extent.

3. Whenever the number of beats of the heart is considerably increased from any cause, the quantity of blood discharged at each ventricular systole is very much diminished, either from lack of complete distention or from imperfect emptying of the cavities.

Phenomena in the Circulatory System after Death.—We do not believe that any one has proven the existence of a force in the capillaries or the tissues (capillary power) which materially assists the circulation during life or produces any movement immediately after death; and we shall not, therefore, discuss the extraordinary post-mortem phenomena of circulation, particularly those which have been observed by Dr. Dowler in subjects dead of yellow fever. But nearly every autopsy shows that, after death, the blood does not remain equally distributed in the arteries, capillaries, and veins. Influenced by gravitation, it accumulates in and discolors the most dependent parts of the body. The arteries are always found empty, and all the blood in the body accumulates in the venous system and capillaries; a fact which was observed by the ancients and gave rise to the belief that the arteries, as their name implies, were air-bearing tubes. This has long engaged the attention of physiologists, who have attempted to explain it by various theories. Without discussing the views on this subject anterior to our knowledge of the great contractile power of the arteries as compared with other vessels, we may cite the following experiment of Magendie as offering a satisfactory explanation. If the artery and vein of a limb be exposed in a living animal and all the other vessels be tied, compression of the artery does not immediately arrest the current in the vein, but the blood will continue to flow until the artery is entirely emptied. The artery, when relieved from the distending force of the heart, reacts on its contents by virtue of its contractile coat and completely empties itself of blood. An action similar to this takes place after death throughout the entire arterial system. The vessels react on their contents and gradually force all the blood into and through the capillaries, which are very short, to the veins, which are capacious, distensible, and but slightly contractile. This begins immediately after death, while the irritability of the muscular coat of the arteries remains, and is seconded by the subsequent cadaveric rigidity, which affects all the involuntary, as well as the voluntary muscular fibres. Once in the venous system, the blood cannot return on account of the valves. Thus, after death, the blood is found in the veins and capillaries of dependent parts of the body.

CHAPTER IV.

RESPIRATION—RESPIRATORY MOVEMENTS.

General considerations—Physiological anatomy of the respiratory organs—Respiratory movements of the larynx—Epiglottis—Trachea and bronchial tubes—Parenchyma of the lungs—Movements of respiration—Inspiration—Muscles of inspiration—Expiration—Influence of the elasticity of the pulmonary structure and walls of the chest upon expiration—Muscles of expiration—Action of the abdominal muscles in expiration—Types of respiration—Frequency of the respiratory movements—Relations of inspiration and expiration to each other—The respiratory sounds—Capacity of the lungs and the quantity of air changed in the respiratory acts—Residual air—Reserve air—Tidal, or breathing air—Complemental air—Extreme breathing capacity—Relations in volume of the expired to the inspired air—Diffusion of air in the lungs.

The characters of the blood are by no means identical in the three great divisions of the vascular system; but physiologists have thus far been able to investigate only the differences which exist between arterial and venous blood, for the capillaries are so short, communicating directly with the arteries on the one side and the veins on the other, that it is impossible to obtain a specimen of true capillary blood. In the capillaries, however, the nutritive fluid, which is identical in all parts of the arterial system, undergoes a remarkable change, which renders it unfit for nutrition. Thus modified it is known as venous blood; and, as we have seen, the only office of the veins is to carry it back to the right side of the heart, to be sent to the lungs, where it loses the vitiating materials it has collected in the tissues, takes in a fresh supply of oxygen, and goes to the left, or systemic heart, again prepared for nutrition. As the processes of nutrition vary in different parts of the organism, there are of necessity corresponding variations in the composition of the blood throughout the venous system.

The important principles which are given off by the lungs are exhaled from the blood; and the gas which disappears from the air is absorbed by the blood, mainly by its corpuscular elements.

A proper supply of oxygen is indispensable to nutrition and even to the comparatively-mechanical process of circulation; but it is no less necessary to the nutritive processes that carbonic acid, which the blood acquires in the tissues, should be given off.

Respiration may be defined strictly as the process by which the various tissues and organs receive and appropriate oxygen.

As it is almost exclusively through the blood that the tissues and organs are supplied with oxygen, and as the blood receives and exhales most of the carbonic acid, the respiratory process may be said to consist chiefly in the change of venous into arterial blood. But experiments have demonstrated that the tissues themselves, detached from the body and placed in an atmosphere of oxygen, will absorb this gas and exhale carbonic acid. Under these circumstances, they certainly respire; and it is evident, therefore, that, in this process, the intervention of the blood is not an absolute necessity.

The tide of air in the lungs does not constitute respiration, as we now understand it. These organs merely serve to facilitate the introduction of oxygen into the blood and the exhalation of carbonic acid. If the system be drained of blood, or if the blood be rendered incapable of interchanging its gases with the air, respiration ceases, and all the phenomena of asphyxia are presented, although air be introduced into the lungs with perfect regularity. It must be remembered that the essential processes of respiration take place in all the tissues and organs of the system and not in the lungs. Respiration is a process similar to what are known as the processes of nutrition; and, although it is much more active and uniform than the ordinary nutritive acts, it is inseparably connected with, and strictly a part of the general process. As, in the nutrition of the substance of tissues, the nitrogenized principles of the blood united with inorganic matters are used up, transformed into the tissue itself, finally changed into excrementitious products, such as urea or cholesterine, and discharged from the body, so the oxygen of the blood is appropriated, and carbonic acid, which is an excrementitious product, is produced, whenever tissues are worn out and regenerated. There is a necessary and inseparable connection between all these processes; and they must be considered, not as distinct functions, but as different parts of the one great function of nutrition. As we are as yet unable to follow out all the intermediate changes which take place between the appropriation of nutritive materials from the blood and the production of effete or excrementitious substances, it is impossible to say precisely how oxygen is used by the tissues and how carbonic acid is produced. We only know that more or less oxygen is necessary for the nutrition of all tissues, in all animals, high or low in the scale, and that the tissues produce a certain quantity of carbonic acid. The fact that oxygen is consumed with much greater rapidity than any other nutritive principle and that the production of carbonic acid is correspondingly active, as compared with other effete products, points pretty conclusively to a connection between the absorption of the one principle and the production of the other.

In some of the lowest of the inferior animals, there is no special respiratory organ, the interchange of gases being effected through the general surface. Higher in the animal scale, special organs are found, which are called gills when the animals live under water and respire the air which is in solution in the water, and lungs when the air is introduced in a gaseous form. Animals possessed of lungs have a tolerably-perfect circulatory apparatus, so that the blood is made to pass continually through the respiratory organs. In the human subject and the warm-blooded animals generally, the lungs are very complex and present an immense surface by which the blood is exposed to the air, separated from it simply by a delicate and permeable membrane. These animals are likewise provided with a special heart, which has the function of carrying on the pulmonary circulation. Although respiration is carried on to some extent by the general surface, the lungs are the important and essential organs in which the interchange of gases takes place.

The essential conditions for respiration in animals which have a circulating nutritive fluid are: air and blood, separated by a membrane which will allow the passage of gases. The effete products of respiration in the blood pass out and vitiate the air. The air is deprived of a certain portion of its oxygen, which passes into the blood, to be conveyed to the tissues. Thus the air must be changed to supply fresh oxygen and get rid of the carbonic acid. The rapidity of this change is in proportion to the nutritive activity of the animal and the rapidity of the circulation of the blood.

In treating in detail of the function of respiration, it will be convenient to make the following division of the subject:

1. The mechanical phenomena of respiration; or the processes by which the fresh air is introduced into the lungs (inspiration), and the vitiated air is expelled (expiration).

2. The changes which the air undergoes in respiration.

3. The changes which the blood undergoes in respiration.

4. The relations of the consumption of oxygen and the production of carbonic acid to the general process of nutrition.

5. The respiratory sense; a want, on the part of the system, which induces the respiratory acts (*besoin de respirer*).

6. Cutaneous respiration.

7. Asphyxia.

The study of these questions will be facilitated by a brief consideration of some points in the anatomy of the respiratory organs.

Physiological Anatomy of the Respiratory Organs.

Passing backward from the mouth to the pharynx, two openings are observed; a posterior opening, which leads to the œsophagus, and an anterior opening, the opening of the larynx, which is the commencement of the passages devoted exclusively to respiration. The structure of the œsophagus and of the air-tubes is entirely different. The œsophagus is flaccid and destined to receive and convey to the stomach the articles of food, which are introduced by the constrictions of the muscles above. The trachea and its ramifications are exclusively for the passage of air, which is taken in by a suction force produced by the enlargement of the thorax. The act of inhalation requires that the tubes should be kept open by walls sufficiently rigid to resist the external pressure of the air.

Beginning our description with the larynx, it is seen that the cartilages of which it is composed are sufficiently rigid and unyielding to resist the pressure produced by any inspiratory effort. Across its superior opening are the vocal chords, which are four in number and have a direction from before backward. The two superior are called the false vocal chords, because they are not concerned in the production of the voice. The two inferior are the true vocal chords. They are ligamentous bands covered by folds of mucous membrane, which is quite thick on the superior chords and very thin and delicate on the inferior. Anteriorly, they are attached to a fixed point between the thyroid cartilages, and posteriorly, to the movable arytenoid cartilages. Air is admitted to the trachea through an opening between the chords, which is called the rima glottidis. Little muscles, arising from the thyroid and cricoid and attached to the arytenoid cartilages, are capable of separating and approximating the points to which the vocal chords are attached posteriorly, so as to open and close the rima glottidis.

If the glottis be exposed in a living animal, certain regular movements are presented, which are synchronous with the acts of respiration. The larynx is opened at each inspiration by the action of the muscles referred to above, so that the air has a free entrance to the trachea. At the termination of the inspiratory act, these muscles are relaxed, the vocal chords fall together by their own elasticity, and, in expiration, the chink of the glottis returns to the condition of a narrow slit. These respiratory movements of the glottis are constant and are essential to the introduction of air in proper quantity into the lungs. The expulsion of air from the lungs is rather a passive process and tends in itself to separate the vocal chords; but inspiration, which is active and more violent, were it not for the movements of the glottis, would have a tendency to draw the vocal chords together. The muscles which are concerned in producing these movements are animated by the inferior laryngeal branches of the pneumogastric nerves. If these nerves be divided, the movements of the glottis are arrested, and respiration is very seriously interfered with. This is particularly marked in young animals, in which the walls of the larynx are comparatively yielding, when the operation is frequently followed by immediate death from suffocation. The movements of the glottis enable us to understand how foreign bodies of considerable size are sometimes accidentally introduced into the air-passages. The respiratory movements of the larynx are entirely distinct from those concerned in the production of the voice and are simply for the purpose of facilitating the entrance of air in respiration.

Attached to the anterior portion of the larynx, is the epiglottis, a little, leaf-shaped lamella of fibro-cartilage, which, during ordinary respiration, projects upward and lies against the posterior portion of the tongue. During the act of deglutition, respiration is momentarily interrupted, and the air-passages are protected by the tongue, which presses backward, carrying the epiglottis before it and completely closing the opening of the

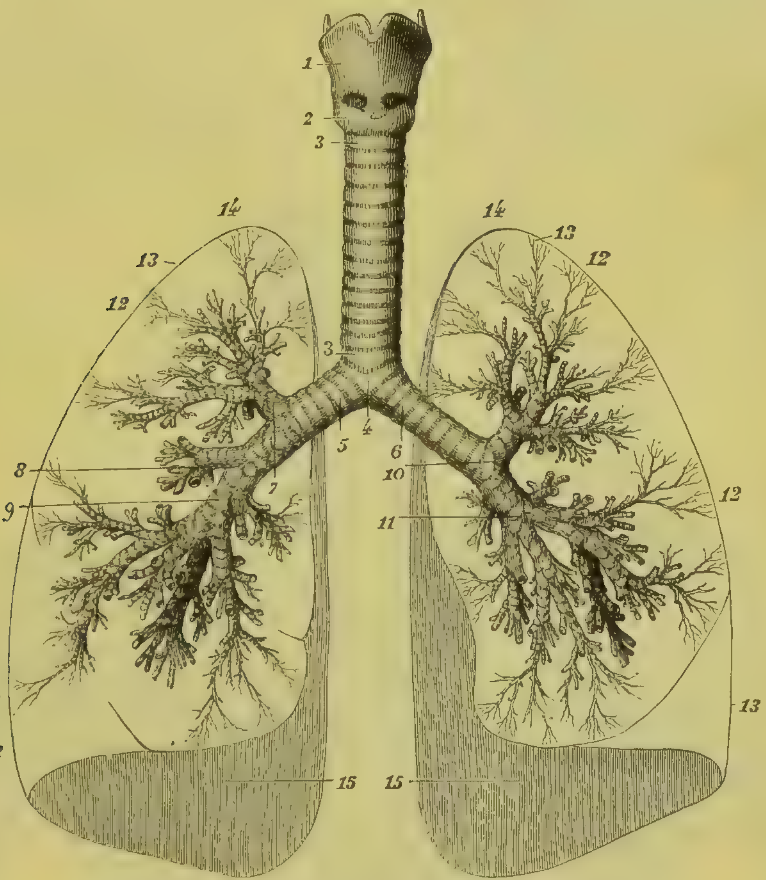


FIG. 35.—*Trachea and bronchial tubes.* (Sappey.)

1, 2, larynx; 3, 3, trachea; 4, bifurcation of the trachea; 5, right bronchus; 6, left bronchus; 7, bronchial division to the upper lobe of the right lung; 8, division to the middle lobe; 9, division to the lower lobe; 10, division to the upper lobe of the left lung; 11, division to the lower lobe; 12, 12, 12, 12, ultimate ramifications of the bronchi; 13, 13, 13, 13, lungs, represented in contour; 14, 14, summit of the lungs; 15, 15, base of the lungs.

larynx. Physiologists have questioned whether the epiglottis be necessary to the complete protection of the air-passages; and, repeating the experiments of Magendie, it has been frequently removed from the lower animals without apparently interfering with the proper deglutition of solids or liquids. We have been satisfied, from actual experiment, that a dog will swallow liquids and solids immediately after the ablation of the epiglottis, without allowing any to pass into the trachea; but it becomes a question whether this experiment can be absolutely applied to the human subject. In a case of loss of the entire epiglottis, which was observed in the Bellevue Hospital, the patient experienced slight difficulty in swallowing, from the passage of little particles into the larynx, which produced cough. This case seemed to show that the presence of the epiglottis, in the human subject at least, is necessary to the complete protection of the air-passages in deglutition.

Passing down the neck from the larynx toward the lungs, is a tube, from four to four and a half inches in length and about three-quarters of an inch in diameter, which is called the trachea. It is provided with cartilaginous rings, from sixteen to twenty in number, which partially surround the tube, leaving about one-third of its posterior portion occupied by fibrous tissue mixed with a certain number of non-striated muscular fibres. Passing into the chest, the trachea divides into the two primitive bronchi, the right being shorter, larger, and more horizontal than the left. These tubes, provided, like the trachea, with imperfect cartilaginous rings, enter the lungs, divide and subdivide, until the minute ramifications of the bronchial tree open directly into the air-cells. After penetrating the lungs, the cartilages become irregular and are in the form of oblong, angular plates, which are so disposed as to completely encircle the tubes. In tubes of very small size, these plates are less numerous than in the larger bronchi, until, in tubes of a less diameter than $\frac{1}{50}$ of an inch, they are lost altogether.

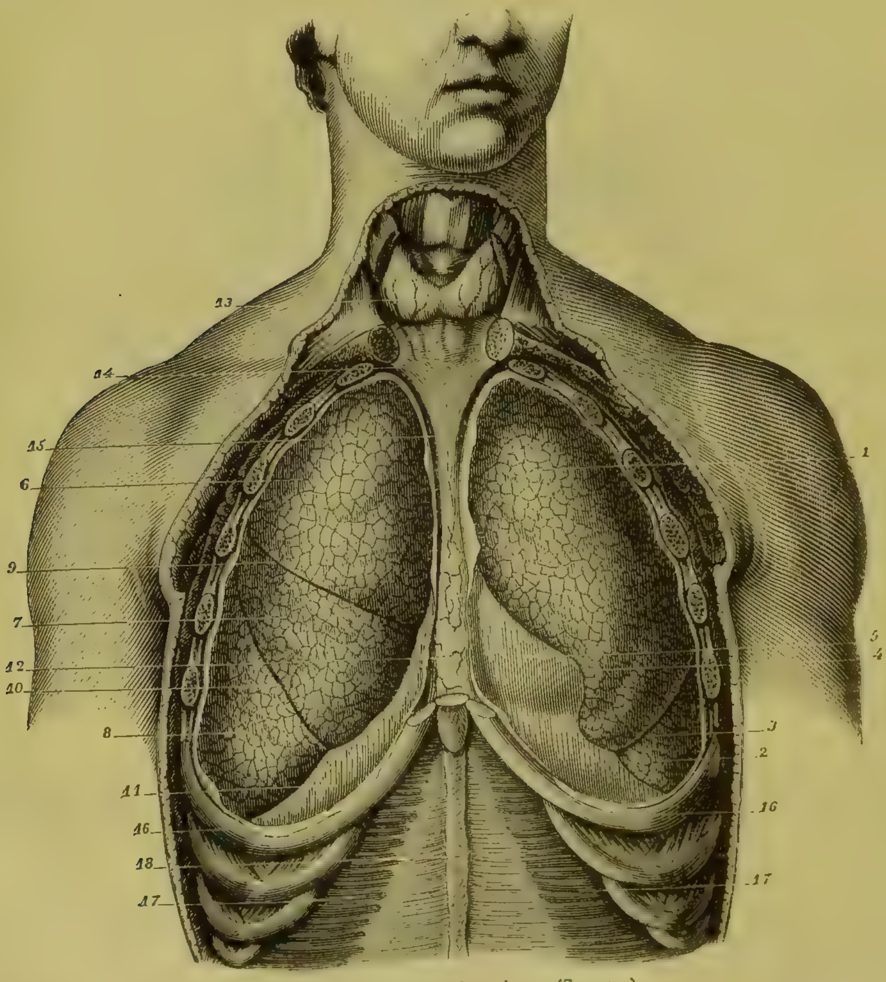


FIG. 36.—*Lungs, anterior view.* (Sappey.)

1, *upper lobe of the left lung*; 2, *lower lobe*; 3, *fissure*; 4, *notch corresponding to the apex of the heart*; 5, pericardium; 6, *upper lobe of the right lung*; 7, *middle lobe*; 8, *lower lobe*; 9, *fissure*; 10, *fissure*; 11, diaphragm; 12, anterior mediastinum; 13, thyroid gland; 14, middle cervical aponeurosis; 15, process of attachment of the mediastinum to the pericardium; 16, 16, seventh ribs; 17, 17, transversales muscles; 18, linea alba.

The walls of the trachea and bronchial tubes are composed of two distinct membranes; an external membrane, between the layers of which the cartilages are situated, and a lining mucous membrane. The external membrane is composed of inelastic and elastic fibrous tissue. Posteriorly, in the space not covered by cartilaginous rings, these fibres are mixed with a certain number of unstriped, or involuntary muscular fibres, which exist in two layers; a thick internal layer, in which the fibres are transverse, and a thinner longitudinal layer, which is external. This collection of muscular fibres is sometimes called the trachealis muscle. Throughout the entire system of bronchial tubes, there are circular fasciculi of muscular fibres lying just beneath the mucous membrane, with a number of longitudinal elastic fibres. The character of the bronchi abruptly changes in tubes less than $\frac{1}{50}$ of an inch in diameter. They lose the cartilaginous rings, and the external and the mucous membranes become so closely united that they can no longer be separated by dissection. The circular muscular fibres continue down to the air-cells. The mucous membrane is smooth, covered by ciliated epithelium, the movements of the cilia being always from within outward, and it is provided with numerous mucous glands. These glands are of the racemose variety and, in the larynx, are of considerable size. In the trachea and bronchi, racemose glands exist in the membrane on the posterior surface of the tubes; but anteriorly are small follicles, terminating in a single, and sometimes a double, blind extremity. These follicles are lost in tubes measuring less than $\frac{1}{50}$ of an inch in diameter.

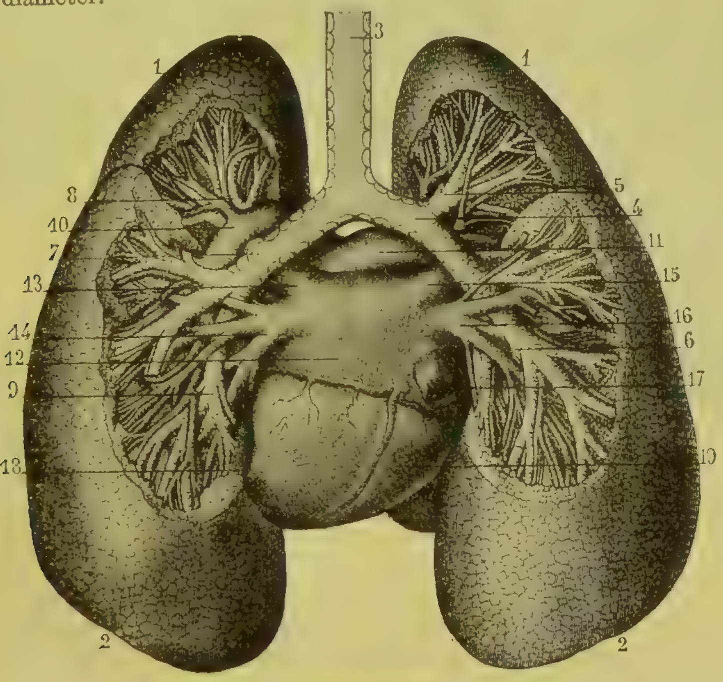


FIG. 37.—*Bronchi and lungs, posterior view.* (Sappey.)

1, 1, *summit of the lungs*; 2, 2, *base of the lungs*; 3, *trachea*; 4, *right bronchus*; 5, *division to the upper lobe of the lung*; 6, *division to the lower lobe*; 7, *left bronchus*; 8, *division to the upper lobe*; 9, *division to the lower lobe*; 10, left branch of the pulmonary artery; 11, right branch; 12, left auricle of the heart; 13, left superior pulmonary vein; 14, left inferior pulmonary vein; 15, right superior pulmonary vein; 16, right inferior pulmonary vein; 17, inferior vena cava; 18, left ventricle of the heart; 19, right ventricle.

It is the anatomy of the parenchyma of the lungs which possesses the most physiological interest, for here the essential processes of respiration take place. When moderately inflated, the lungs have the appearance of irregular cones, with rounded apices, and concave bases resting upon the diaphragm. They fill all of the cavity of the chest which is not occupied by the heart and great vessels, and are completely separated from each other by the mediastinum. In the human subject, the lungs are not attached to the thoracic walls, but are closely applied to them, each covered by a reflection of the serous membrane which lines the cavity of the corresponding side. Thus they necessarily follow the movements of expansion and contraction of the thorax. Deep fissures divide the right lung into three lobes and the left lung into two. The surface of the lungs is divided into irregularly-polygonal spaces, from $\frac{1}{4}$ of an inch to an inch in diameter, which mark what are sometimes called the pulmonary lobules; although this term is incorrect, as each of these divisions includes quite a number of the true lobules.

Following out the bronchial tubes from the diameter of $\frac{1}{50}$ of an inch, the smallest, which are from $\frac{1}{120}$ to $\frac{1}{75}$ of an inch in diameter, open into a collection of oblong vesicles, which are the air-cells. Each collection of vesicles constitutes one of the true pulmonary lobules and is from $\frac{1}{50}$ to $\frac{1}{12}$ of an inch in diameter. After entering the lobule, the tube forms a sort of tortuous central canal, sending off branches which terminate in groups of from eight to fifteen pulmonary cells. The cells are a little deeper than they are wide and have each a rounded, blind extremity. Some are smooth, but many are marked by little circular constrictions, or rugæ. In the healthy lung of the adult, after death, they measure from $\frac{1}{200}$ to $\frac{1}{120}$ or $\frac{1}{70}$ of an inch in diameter, but are capable of very great distention. The smallest cells are in the deep portions of the lungs, and the largest are situated near the surface. There are considerable variations in the size of the cells at different periods of life. The smallest cells are found in young children, and they progressively increase in size with age. The walls of the air-cells contain numerous small elastic fibres, which do not form distinct bundles for each air-cell, but anastomose freely with each other, so that the same fibres belong to two or more cells. This structure is peculiar to the parenchyma of the lungs and gives to these organs their great distensibility and elasticity, properties which play an important part in expelling the air from the chest, as a consequence simply of cessation of the action of the inspiratory muscles. Interwoven with these elastic fibres, is the richest plexus of capillary blood-vessels found in the economy. The vessels are larger than the capillaries in other situations, and the plexus is so close that the spaces between them are narrower than the vessels themselves. When distended, the blood-vessels form the greatest part of the walls of the cells.

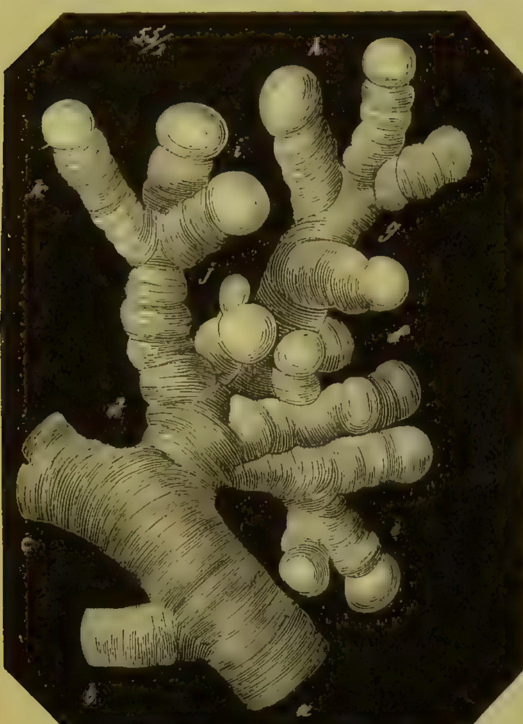


FIG. 88.—*Mould of a terminal bronchus and a group of air-cells moderately distended by injection, from the human subject.* (Robin.)

Lining the air-cells, are very thin scales of pavement-epithelium, from $\frac{1}{2500}$ to $\frac{1}{2000}$ of an inch in diameter, which are applied directly to the walls of the blood-vessels. The epithelium here does not seem to be regularly desquamated, as in other situations. Examination of injected specimens shows that the blood-vessels are so situated between the cells, that the blood in the greater part of their circumference is exposed to the action of the air.

The entire mass of venous blood is distributed in the lungs by the pulmonary artery. Arterial blood is conveyed to these organs by the bronchial arteries, which ramify and subdivide on the bronchial tubes and follow their course into the lungs, for the nourishment of these parts. It is possible that the tissue of the lungs may receive some nourishment from the blood conveyed there by the pulmonary artery; but, as this vessel does not send any branches to the bronchial tubes, it is undoubtedly the bronchial arteries which supply the material for their nutrition and for the secretion of the mucous glands. This is one of the anatomical reasons why inflammatory conditions of the bronchial tubes do not extend to the parenchyma of the lungs, and *vice versa.*

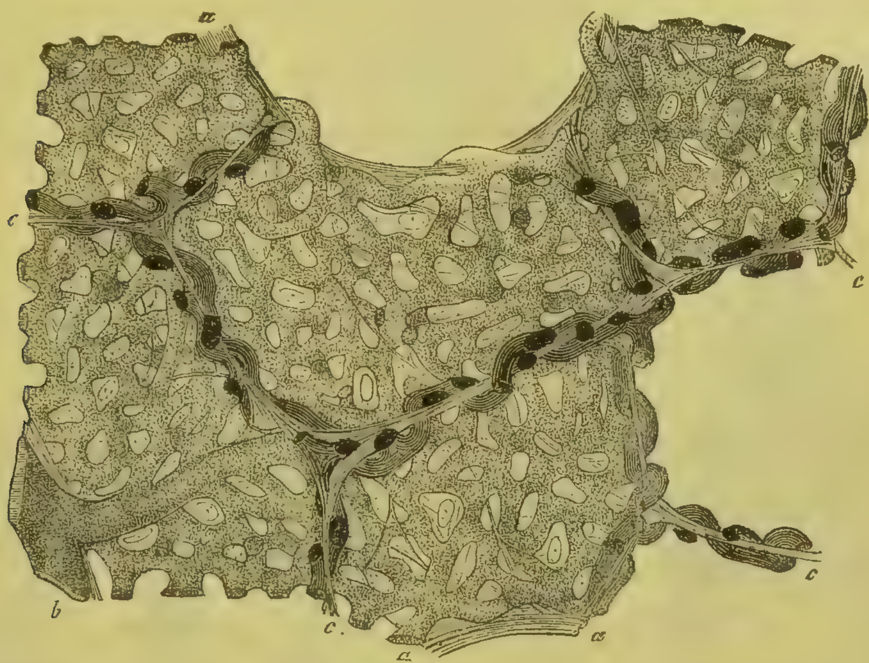


FIG. 39.—*Section of the parenchyma of the human lung, injected through the pulmonary artery.* (Schulze.) *a, a, c, c,* wall of the air-cell; *b,* small arterial branch.

The foregoing anatomical sketch shows the admirable adaptation of the trachea and bronchial tubes to the passage of the air by inspiration to the deep portions of the lungs, and the favorable conditions which it there meets with for an interchange of the elements of the air and blood. It is also evident, from the enormous number of air-cells, that the respiratory surface must be immense.[1]

Movements of Respiration.

In man and in the warm-blooded animals generally, inspiration takes place as a consequence of enlargement of the thoracic cavity and the entrance of a quantity of air through the respiratory passages corresponding to the increased capacity of the lungs. In the mammalia, the chest is enlarged by the action of muscles; and, in ordinary respiration, inspiration is an active process, while expiration is comparatively passive.

A glance at the physiological anatomy of the thorax in the human subject makes it evident that the action of certain muscles will considerably increase its capacity. In the first place, the diaphragm mounts up into its cavity in the form of a vaulted arch. By contraction of its fibres, it is brought nearer a plane, and thus the vertical diameter of the thorax is increased. The walls of the thorax are formed by the dorsal vertebræ and

[1] Hales estimated the combined surface of the air-cells at 289 square feet; Keill, at about 152 square feet; and Lieberkühn, at 1,500 square feet. There are not sufficient data on this point for us to form any thing like a reliable estimate. It is simply evident that the extent of surface must be very great. In passing from the lower to the higher orders of animals, it is seen that Nature provides for the necessity of an increase in the activity of the respiratory process, by a diminished size and a multiplication of the air-cells.

ribs posteriorly, by the upper ten ribs laterally, and by the sternum and costal cartilages anteriorly. The direction of the ribs, their mode of connection with the sternum by the costal cartilages, and their articulation with the vertebral column, are such that, by their movements, the antero-posterior and transverse diameters of the chest may be considerably modified.

Inspiration.

The ribs are somewhat twisted upon themselves and have a general direction forward and downward. The first rib is nearly horizontal, but the obliquity of the ribs progressively increases from the upper to the lower parts of the chest. They are articulated with the bodies of the vertebræ, so as to allow of considerable motion. The upper seven ribs are attached by the costal cartilages to the sternum, these cartilages running upward and

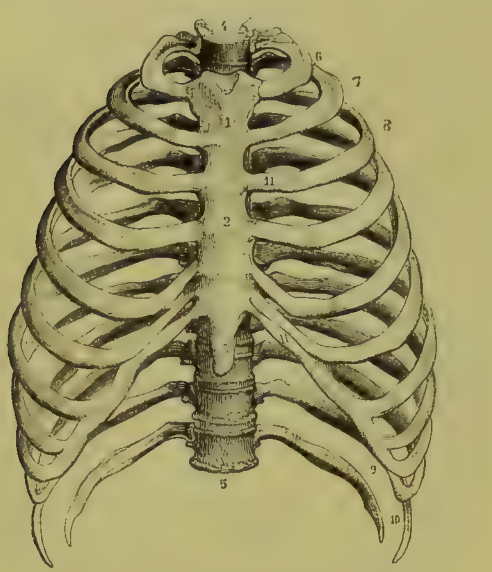


FIG. 40.—*Thorax, anterior view.* (Sappey.)

1, 2, 3, sternum; 4, circumference of the upper portion of the thorax; 5, circumference of the base of the thorax; 6, first rib; 7, second rib; 8, 8, last five sternal ribs; 9, upper three false ribs; 10, last two, or floating ribs; 11, costal cartilages.

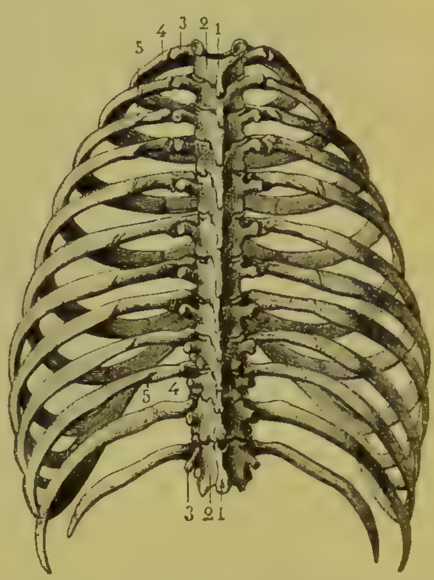


FIG. 41.—*Thorax, posterior view.* (Sappey.)

1, 1, spinous processes of the dorsal vertebræ; 2, 2, laminæ of the vertebræ; 3, 3, transverse processes; 4, 4, dorsal portions of the ribs; 5, 5, angles of the ribs.

inward. The cartilages of the eighth, ninth, and tenth ribs are joined to the cartilage of the seventh. The eleventh and twelfth are floating ribs and are attached only to the vertebræ.

It may be stated, in general terms, that inspiration is effected by descent of the diaphragm and elevation of the ribs; and expiration, by elevation of the diaphragm and descent of the ribs.

Arising severally from the lower border of each rib and attached to the upper border of the rib below, are the eleven external intercostal muscles, the fibres of which have an oblique direction from above downward and forward. Attached to the inner borders of the ribs are the internal intercostals, which have a direction from above downward and backward, nearly at right angles to the fibres of the external intercostals. There are also a number of muscles attached to the thorax and spine, thorax and head, upper part of humerus, etc., which are capable of elevating either the entire chest or the ribs. These must act as muscles of inspiration, when the attachments to the thorax become the movable points. Some of them are called into action during ordinary respiration; others act as auxiliaries when respiration is a little exaggerated, as after exercise, and are called ordinary auxiliaries; while others, which ordinarily have a different function, are only brought into play when respiration is excessively difficult, and are called extraordinary auxiliaries.

The following are the principal muscles concerned in inspiration:

Muscles of Inspiration.

Ordinary Respiration.

Muscle.	*Attachments.*
Diaphragm	Circumference of lower border of thorax.
Scalenus anticus	Transverse processes of third, fourth, fifth, and sixth cervical vertebræ——tubercle of first rib.
Scalenus medius	Transverse processes of lower six cervical vertebræ——upper surface of first rib.
Scalenus posticus	Transverse processes of lower two or three cervical vertebræ——outer surface of second rib.
External intercostals	Outer borders of the ribs.
Sternal portion of internal intercostals	Borders of the costal cartilages.
Twelve levatores costarum	Transverse processes of dorsal vertebræ——ribs, between the tubercles and angles.

Ordinary Auxiliaries.

Serratus posticus superior	Ligamentum nuchæ, spinous processes of last cervical and upper two or three dorsal vertebræ——upper borders of second, third, fourth, and fifth ribs, just beyond the angles.
Sterno-mastoideus	Upper part of sternum——mastoid process of temporal bone.

Extraordinary Auxiliaries.

Levator anguli scapulæ	Transverse processes of upper three or four cervical vertebræ——posterior border of superior angle of scapula.
Trapezius (superior portion)	Ligamentum nuchæ and seventh cervical vertebra——upper border of spine of scapula.
Pectoralis minor	Coracoid process of scapula——anterior surface and upper margins of third, fourth, and fifth ribs, near the cartilages.
Pectoralis major (inferior portion)	Bicipital groove of humerus——costal cartilages and lower part of sternum.
Serratus magnus	Inner margin of posterior border of scapula——external surface and upper border of upper eight ribs.

Action of the Diaphragm.—The descriptive and general anatomy of the diaphragm gives a pretty correct idea of its functions in respiration. It arises, anteriorly, from the inner surface of the ensiform cartilage, laterally, from the inner surface of the lower borders of the costal cartilages and the six or seven inferior ribs, passes over the quadratus lumborum by the external arcuate ligament, and the psoas magnus by the internal arcuate ligament, and has two tendinous slips of origin, called cruræ of the diaphragm, from the bodies of the second, third, and fourth lumbar vertebræ and the intervertebral cartilages on the right side, and the second and third lumbar vertebræ and the intervertebral cartilages on the left side. From this origin, which extends around the lower circumference of the thorax, it mounts into the cavity of the chest, forming a vaulted arch, or dome, with its concavity toward the abdomen and its convexity toward the lungs. In the central portion, there is a tendon of considerable size and shaped something like the club on a playing-card, with middle, right, and left leaflets. The remainder of the organ is composed of radiating fibres of voluntary muscular tissue. The œsophagus, aorta, and inferior vena cava pass through the diaphragm from the thoracic to the abdominal cavity, by three openings.

The opening for the œsophagus is surrounded by muscular fibres, by which it is partially closed when the diaphragm contracts in inspiration, as the fibres simply surround the tube, and none are attached to it.

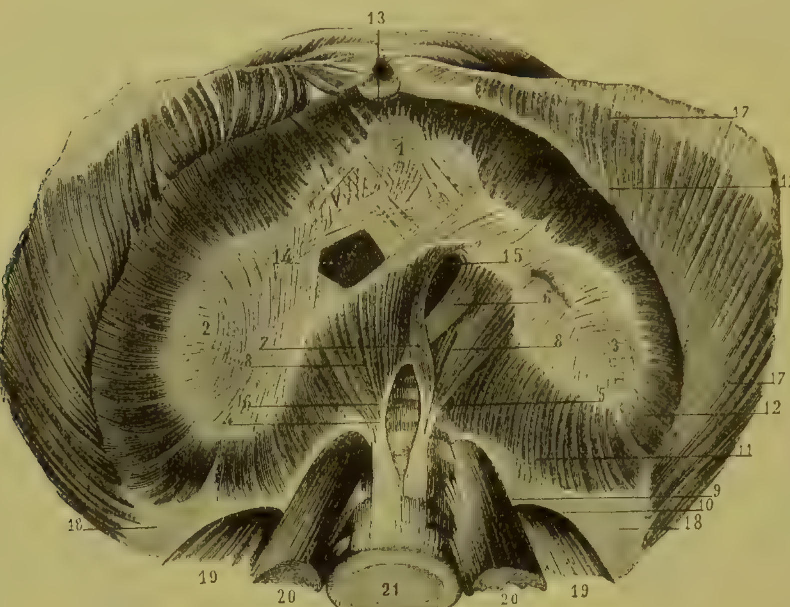


FIG. 42.—*Diaphragm.* (Sappey.)

1, 2, 3, central tendon; 4, right pillar; 5, left pillar; 6, 7, processes between the pillars; 8, 8, openings for the splanchnic nerves; 9, fibrous arch passing over the psoas magnus; 10, fibrous arch passing over the quadratus lumborum; 11, muscular fibres arising from these two arches; 12, 12, muscular fibres arising from the lower six ribs; 13, fibres from the ensiform cartilage; 14, opening for the vena cava; 15, opening for the œsophagus; 16, opening for the aorta; 17, 17, part of the transversalis muscle; 18, 18, aponeurosis; 19, 19, quadratus lumborum; 20, 20, psoas magnus; 21, fourth lumbar vertebra.

The orifice for the aorta is bounded by the bone and aponeurosis posteriorly, and in front, by a fibrous band to which the muscular fibres are attached, so that their contraction has a tendency rather to increase than to diminish the caliber of the vessel.

The orifice for the vena cava is surrounded entirely by tendinous structure, and contraction of the diaphragm, although it might render the form of the orifice more nearly circular, can have no effect upon its caliber.

The action of the diaphragm can be easily studied in the inferior animals by vivisections. If the abdomen of a cat, which, from the conformation of the parts, is well adapted to this experiment, be largely opened, we can observe the descent of the tendinous portion and the contraction of the muscular fibres. The action of this muscle may be rendered more apparent by compressing the walls of the chest with the hands, so as to interfere somewhat with the movements of the ribs. By putting a strong ligature around the spinal column and soft parts just below the diaphragm and cutting off the lower half of the body, as was done by the assistant to the chair of physiology in the Bellevue Hospital Medical College, Dr. C. F. Roberts, the movements of the diaphragm may be very beautifully exhibited in class-demonstrations.

In ordinary respiration, the descent of the diaphragm and its approximation to a plane are the chief phenomena observed; but, as there is a slight resistance to the depression of the central tendon, it is probable that there is also a certain amount of elevation of the inferior ribs, the diaphragm assisting, in a limited degree it is true, the action of the external intercostals.

The phenomena referable to the abdomen, which coincide with the descent of the diaphragm, can easily be observed in the human subject. As the diaphragm is depressed, it necessarily pushes the viscera before it, and inspiration is therefore accompanied by protrusion of the abdomen. This may be rendered very marked by a forced or deep inspiration.

The action of the diaphragm may be illustrated by a very simple yet striking experiment. In an animal just killed, after opening the abdomen, if we take hold of the structures which are attached to the central tendon and make traction, we imitate, in a rough way, the movements of the diaphragm in respiration, and the air will pass into the lungs, sometimes with a distinctly-audible sound.

The effects of the action of the diaphragm upon the size of its orifices are chiefly limited to the œsophageal opening. The anatomy of the parts is such that contraction of the muscular fibres has a tendency to close this orifice. When we come to treat of the digestive system, we shall see that the contraction of the diaphragm is auxiliary to the action of the muscular walls of the œsophagus itself, by which the cardiac opening of the stomach is regularly closed during inspiration. This may become important when the stomach is much distended; for descent of the diaphragm compresses all the abdominal organs and might otherwise cause regurgitation of food.

The contractions of the diaphragm are animated almost exclusively, if not exclusively, by the phrenic nerve; a nerve which, having the office of supplying the most important respiratory muscle, derives its filaments from a number of sources. It arises from the third and fourth cervical nerves, receiving a branch from the fifth and sometimes from the sixth; it passes through the chest, penetrates the diaphragm, and is distributed to its under surface. This nerve was the subject of numerous experiments by the early physiologists, who were greatly interested in the minutiæ of the action of the diaphragm and of other muscles, in respiration. Its galvanization produces convulsive contractions of the diaphragm, and its section paralyzes the muscle almost completely. It was noticed by Lower, that after section of both phrenic nerves the movements of the abdomen were reversed, and it became retracted in inspiration. This is explained and illustrated by voluntary suspension of the action of the diaphragm and exaggeration of the costal movements. As the ribs are raised, the atmospheric pressure causes the diaphragm to mount up into the cavity of the thorax, and of course the abdominal organs follow.

From the great increase in the capacity of the chest produced by the action of the diaphragm and its constant and universal action in respiration, it must be regarded as by far the most important and efficient of the muscles of inspiration.

Hiccough, sobbing, laughing, and crying, are due mainly to the action of the diaphragm, particularly hiccough and sobbing, which are produced by spasmodic contractions of this muscle, generally beyond the control of the will.

Action of the Muscles which elevate the Ribs.—Scalene Muscles.—In ordinary respiration, the ribs and the entire chest are elevated by the combined action of a number of muscles. The three scalene muscles are attached to the cervical vertebræ and the first and second ribs. These muscles, which act particularly upon the first rib, must elevate with it, in inspiration, the rest of the thorax. The articulation of the first rib with the vertebral column is very movable, but it is joined to the sternum by a very short cartilage, which allows of very little movement, so that its elevation necessarily carries with it the sternum. This movement increases both the transverse and antero-posterior diameters of the thorax, from the mode of articulation and direction of the ribs, which are somewhat rotated as well as rendered more horizontal.

Intercostal Muscles.—Concerning the mechanism of the action of these muscles, there is great difference of opinion among physiologists; so much, indeed, that the author of a late elaborate work assumes that the question is still left in considerable uncertainty. The most extended researches on this point are those of Beau and Maissiat (*Archives générales de médecine*, 1843), and Sibson (*Philosophical Transactions*, 1846). The latter seem to settle the question of the mode of action of the intercostals and explain satisfactorily certain points which even now are not generally appreciated. More recently, Onimus has shown, by experiments upon a decapitated animal, that the external intercostals raise, and the internal intercostals depress the ribs, thus confirming the views of Sibson.

We shall first note the changes which take place in the direction of the ribs and their relation to each other in inspiration, before considering the way in which these movements are produced.

In the dorsal region, the spinal column forms an arch with its concavity toward the chest, and the ribs increase in length progressively, from above downward, to the deepest portion of the arch, where they are longest and then become progressively shorter. According to Sibson, "during inspiration the ribs approach to or recede from each other according to the part of the arch with which they articulate; the four superior ribs approach each other anteriorly and recede from each other posteriorly; the fourth and fifth ribs, and the intermediate set (sixth, seventh, and eighth), move further apart to a moderate, the diaphragmatic set (four inferior), to a great extent. The upper edge of each of these ribs glides toward the vertebræ in relation to the lower edge of the rib above, with the exception of the lowest rib, which is stationary." These movements increase the antero-posterior and transverse diameters of the thorax. As the ribs are elevated and become more nearly horizontal, they must push forward the lower portion of the sternum. Their configuration and mode of articulation with the vertebræ are such, that they cannot be elevated without undergoing a considerable rotation, by which the concavity looking directly toward the lungs is increased, and with it the lateral diameter of the chest. All the intercostal spaces posteriorly are widened in inspiration.

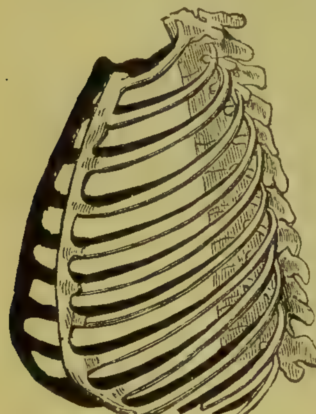


FIG. 43.—*Elevation of the ribs in inspiration.* (Béclard.) The dark lines represent the ribs, sternum, and costal cartilages in inspiration.

The ribs are elevated by the action of the external intercostals, the sternal portion of the internal intercostals, and the levatores costarum. The external intercostals are situated between the ribs only, and are wanting in the region of the costal cartilages. As the vertebral extremities of the ribs are the pivots on which these levers move, and as the sternal extremities are movable, the direction of the fibres of the intercostals from above downward and forward renders elevation of the ribs a necessity of their contraction, if it can be assumed that the first rib is fixed or at least does not move downward. The scalene muscles elevate the first rib in ordinary inspiration; and, in deep inspiration, this takes place to such an extent as to palpably carry with it the sternum and the lower ribs. Theoretically, then, the external intercostals can do nothing but render the ribs more nearly horizontal.

If the external intercostals be exposed in a living animal, the dog, for example, in which the costal type of respiration is very marked, close observation can hardly fail to convince any one that these muscles enter into action in inspiration. This fact has been observed by Sibson and many other physiologists. If attention be directed to the sternal portion of the internal intercostals, situated between the costal cartilages, their fibres having a direction from above downward and backward, it is equally evident that they enter into action with inspiration. By artificially inflating the lungs after death, Sibson confirmed these observations and showed that, when the lungs are filled with air, the fibres of these muscles are shortened. In inspiration, the ribs are all separated posteriorly; but laterally and anteriorly, some are separated (all below the fourth), and some are approximated (all above the fourth). Thus all the interspaces, except the anterior portion of the upper three, are widened in inspiration. Sibson has shown, by inflation of the chest, that, although the ribs are separated from each other, the attachments of the intercostals are approximated. The ribs, from an excessively oblique position, are rendered nearly horizontal; and consequently the inferior attachments of the intercostals are brought nearer the spinal column, while the superior attachments to the upper borders of the ribs are slightly removed from it. Thus these muscles are shortened. If, by separating and elevating the ribs, the muscles be shortened, shortening of the muscles will necessarily elevate and separate the ribs. In the three superior interspaces, the constant direction of the ribs is nearly horizontal, and the course of the intercostal fibres is not so oblique as in those situated between the lower ribs. These spaces are narrowed in inspiration. The muscles between the costal cartilages have a direction opposite to that of the external intercostals and act upon the ribs from the sternum, as the others do from the spinal column. The superior interspace is narrowed, and the remainder are widened, in inspiration.

Levatores Costarum.—The action of these muscles cannot be mistaken. They have immovable points of origin, the transverse processes of twelve vertebræ from the last cervical to the eleventh dorsal, and, spreading out like a fan, are attached to the upper edges of the ribs between the tubercles and the angles. In inspiration, they contract and assist in the elevation of the ribs. They are more developed in man than in the inferior animals.

Auxiliary Muscles of Inspiration.—The muscles which have just been considered are competent to increase the capacity of the thorax sufficiently in ordinary respiration; there are certain muscles, however, which are attached to the chest and the upper part of the spinal column, or upper extremities, which may act in inspiration, although ordinarily the chest is the fixed point and they move the head, neck, or arms. These muscles are brought into action when the movements of respiration are exaggerated. When this exaggeration is but slight and physiological, as after exercise, certain of them (the ordinary auxiliaries) act for a time, until the tranquillity of the movements is restored. But when there is obstruction in the respiratory passages or when respiration is excessively difficult from any cause, threatening suffocation, all the muscles which can by any possibility raise the chest are brought into action. The principal ones are put down in the table under the head of extraordinary auxiliaries. Most of these muscles can voluntarily be brought into play to raise the chest, and the mechanism of their action can in this way be demonstrated.

Serratus Posticus Superior.—This muscle arises from the ligamentum nuchæ, the spinous processes of the last cervical and the upper two or three dorsal vertebræ, its fibres passing obliquely downward and outward, to be attached to the upper borders of the second, third, fourth, and fifth ribs just beyond their angles. By reversing its action, as we have reversed the description of its origin and insertions, it is capable of increasing the capacity of the thorax.

Sterno-mastoideus.—That portion of the muscle which is attached to the mastoid process of the temporal bone and the sternum, when the head is fixed, is capable of acting as a muscle of inspiration. It does not act in ordinary respiration, but its contractions can be readily observed whenever respiration is hurried or exaggerated.

The following muscles, as a rule, act as muscles of inspiration only when respiration is exceedingly difficult or labored. In certain cases of capillary bronchitis, for example, the anxious expression of the countenance betrays the sense of impending suffocation; the head is thrown back and fixed; the shoulders are braced; and every available muscle in brought into action to raise the walls of the thorax.[1]

[1] Under these circumstances, some muscles which we have not thought it necessary to enumerate may act indirectly as muscles of inspiration.

Levator Anguli Scapulæ and Superior Portion of the Trapezius.—Movements of the scapula have often been observed in very labored respiration. Its elevation during inspiration is effected chiefly by the levator anguli scapulæ and the upper portion of the trapezius. The former muscle arises from the transverse processes of the upper three or four cervical vertebræ and is inserted into the posterior border of the scapula below the angle. It is a thick, flat muscle and, when the neck is the fixed point, assists in the elevation of the thorax by raising the scapula. The trapezius is a broad, flat muscle, arising from the occipital protuberance, part of the superior curved line of the occipital bone, the ligamentum nuchæ, and the spinous processes of the last cervical and all the dorsal vertebræ, to be inserted into the upper border of the spine of the scapula. Acting from its attachments to the occiput, the ligamentum nuchæ, the last cervical vertebra, and perhaps one or two of the dorsal vertebræ, this muscle may elevate the scapula and assist in inspiration.

Pectoralis Minor and Inferior Portion of the Pectoralis Major.—These muscles act together to raise the ribs in difficult respiration. The pectoralis minor is the more efficient. Tracing it from its attachment to the coracoid process of the scapula, its fibres pass downward and forward to be attached by three indigitations to the external surface and upper margins of the third, fourth, and fifth ribs just posterior to the costal cartilages. With the coracoid process as the fixed point, this muscle is capable of powerfully assisting in the elevation of the ribs. That portion of the pectoralis major which is attached to the lower part of the sternum and costal cartilages is capable of acting from its insertion into the bicipital groove of the humerus, when the shoulders are fixed, in concert with the pectoralis minor. In great dyspnœa, it is frequently observed that the shoulders are braced, the pectorals acting vigorously to raise the walls of the chest.

Serratus Magnus.—This is a broad, thin muscle covering a great portion of the lateral walls of the thorax. Attached to the inner margin of the posterior border of the scapula, its fibres pass forward and downward and are attached to the external surface and upper borders of the eight superior ribs. Acting from the scapula, this muscle is capable of assisting the pectorals in raising the ribs and becomes a powerful auxiliary in difficult inspiration.

We have thus considered the functions of the principal inspiratory muscles, without taking up those which have an insignificant or undetermined action. In many animals, the nares are considerably distended in inspiration; and, in the horse, which does not respire by the mouth, these movements are as essential to life as the respiratory movements of the larynx. In man, as a rule, the nares undergo no movement unless respiration be somewhat exaggerated. In very difficult respiration, the mouth is opened at each inspiratory act. We have not thought it necessary to treat of the action of those muscles which serve to fix the head, neck, or shoulders in dyspnœa.

The division into muscles of ordinary inspiration, ordinary auxiliaries, and extraordinary auxiliaries, must not be taken as absolute. In the male, in ordinary respiration, the diaphragm, intercostals, and levatores costarum are the great inspiratory muscles, and the action of the scaleni, with the consequent elevation of the sternum, is commonly very slight or may be wanting. In the female, the movements of the upper parts of the chest are very marked, and the scaleni, the serratus posticus superior, and sometimes the sterno-mastoid, are brought into action in ordinary respiration. In the various types of respiration, the action of the muscles engaged in ordinary respiration necessarily presents considerable variations.

Expiration.

The air is expelled from the lungs, in ordinary expiration, by a simple and comparatively-passive process. The lungs contain a great number of elastic fibres surrounding the air-cells and the smallest ramifications of the bronchial tubes, which give them great elasticity. We can form an idea of the extent of elasticity of these organs, by simply removing them from the chest, when they collapse and become many times smaller than the cavity which they before had completely filled. The thoracic walls are also very elastic, particularly in young persons. After the muscles which increase the capacity of the thorax cease their action, the elasticity of the costal cartilages and the tonicity of the muscles which have been put on the stretch will restore the chest to what we may call its passive dimensions. This elasticity is likewise capable of acting as an inspiratory force when the chest has been compressed in any way. There are also certain muscles, the action of which is to draw the ribs downward and which, in tranquil respiration, are antagonistic to those which elevate the ribs. Aside from this, many operations, such as speaking, blowing, singing, etc., require powerful, prolonged, or complicated acts of expiration, in which numerous muscles are brought into play.

Expiration may be considered as depending upon two causes, as follows:

1. The passive influence of the elasticity of the lungs and thoracic walls.

2. The action of certain muscles, which either diminish the transverse and antero-posterior diameters of the chest by depressing the ribs and sternum, or the vertical diameter, by pressing up the abdominal viscera behind the diaphragm.

Influence of the Elasticity of the Pulmonary Structure and Walls of the Chest.—It is easy to understand the influence of the elasticity of the pulmonary structure in expiration. From the collapse of the lungs when openings are made in the chest, it is seen that, even after the most complete expiration, these organs have a tendency to expel part of their gaseous contents, which cannot be fully satisfied until the chest is opened. They remain partially distended, from the impossibility of collapse of the thoracic walls beyond a certain point; and, by virtue of their elasticity, they exert a suction force upon the diaphragm, causing it to form a vaulted arch, or dome above the level of the lower circumference of the chest. When the lungs are collapsed, the diaphragm hangs loosely between the abdominal and thoracic cavities. In inspiration and in expiration, then, the relations between the lungs and diaphragm are reversed. In inspiration, the descending diaphragm exerts a suction force on the lungs, drawing them downward; in expiration, the elastic lungs exert a suction force upon the diaphragm, drawing it upward. This antagonism is one of the causes of the great power of the diaphragm as an inspiratory muscle.

The elasticity of the lungs operates chiefly upon the diaphragm in reducing the capacity of the chest; for the walls of the thorax, by virtue of their own elasticity, have a reaction which succeeds the movements produced by the inspiratory muscles. A simple experiment, which we have often performed in public demonstrations, illustrates the expiratory influence of the elasticity of the lungs. If, in an animal just killed, we open the abdomen, seize hold of the vena cava as it passes through the diaphragm, and make traction, we imitate the action of this muscle sufficiently to produce at times an audible inspiration; on loosing our hold, we have expiration, as it is in a measure accomplished in natural respiration, by virtue of the resiliency of the lungs, carrying the diaphragm up into the thorax. Although this is the main action of the lungs themselves in expiration, their relations to the walls of the thorax are important. By virtue of their elasticity, they assist the passive collapse of the chest. When they lose this property to any considerable extent, as in vesicular emphysema, they offer a notable resistance to the contraction of the thorax; so much, indeed, that in old cases of this disease the movements are much restricted, and the chest presents a characteristic rounded and distended appearance.

Little more need be said concerning the passive movements of the thoracic walls. When the action of the inspiratory muscle ceases, the ribs regain their oblique direction, the intercostal spaces are narrowed, and the sternum, if it have been elevated and drawn forward, falls back to its place simply by virtue of the elasticity of the parts.

Action of Muscles in Expiration.—The following are the principal muscles concerned in expiration:

Muscles of Expiration.

Ordinary Respiration.

Muscle.	*Attachments.*
Osseous portion of internal intercostals	Inner borders of the ribs.
Infracostales	Inner surfaces of the ribs.
Triangularis sterni	Ensiform cartilage, lower borders of sternum, lower three or four costal cartilages——cartilages of the second, third, fourth, and fifth ribs.

Auxiliaries.

Obliquus externus	External surface and inferior borders of eight inferior ribs——anterior half of the crest of the ileum, Poupart's ligament, linea alba.
Obliquus internus	Outer half of Poupart's ligament, anterior two-thirds of the crest of the ileum, lumbar fascia——cartilages of four inferior ribs, linea alba, crest of the pubis, pectineal line.
Transversalis	Outer third of Poupart's ligament, anterior two-thirds of the crest of the ileum, lumbar vertebræ, inner surface of cartilages of six inferior ribs——crest of the pubis, pectineal line, linea alba.
Sacro-lumbalis	Sacrum——angles of six inferior ribs.

Internal Intercostals.—The internal intercostals have different functions in different parts of the thorax. They are attached to the inner borders of the ribs and costal cartilages. Between the ribs, they are covered by the external intercostals, but, between the costal cartilages, they are covered simply by aponeurosis. Their direction is from above downward and backward, nearly at right angles to the external intercostals. The function of that portion of the internal intercostals situated between the costal cartilages has already been noted. They assist the internal intercostals in elevating the ribs in inspiration. Between the ribs, these muscles are directly antagonistic to the external intercostals. They are more nearly at right angles to the ribs, particularly in that portion of the thorax where the obliquity of the ribs is greatest. The observations of Sibson have shown that they are elongated when the chest is distended, and shortened when the chest is collapsed. This fact, taken in connection with experiments on living animals, shows that they are muscles of expiration. Their contraction tends to depress the ribs and consequently to diminish the capacity of the chest. If we bring an animal, a dog for example, completely under the influence of ether, expose the walls of the chest, dissect off the fascia from some of the external intercostals, and then remove carefully a portion of one or two of these muscles so as to expose the fibres of the internal intercostals, it is not difficult, on close examination, to observe the antagonism between the two sets of muscles; one being brought into action in inspiration and the other, in expiration.

Infracostales.—These muscles, situated at the posterior part of the thorax, are variable in size and number. They are most common at the lower part of the chest. Their fibres arise from the inner surface of one rib to be inserted into the inner surface of the first, second, or third rib below. The fibres follow the direction of the internal intercostals, and, acting from their lower attachments, their contractions assist these muscles in drawing the ribs downward.

Triangularis Sterni.—There has never been any doubt concerning the expiratory function of the triangularis sterni. From its origin, the ensiform cartilage, lower borders of the sternum, and lower three or four costal cartilages, it acts upon the cartilages of the second, third, fourth, and fifth ribs, to which it is attached, drawing them downward and thus diminishing the capacity of the chest.

The above-mentioned muscles are called into action in ordinary tranquil respiration, and their sole function is to diminish the capacity of the chest. In labored or difficult expiration, and in the acts of blowing, phonation, etc., other muscles, which are called auxiliaries, play a more or less important part. These muscles all enter into the formation of the walls of the abdomen, and their general action in expiration is to press the abdominal viscera and diaphragm into the thorax and diminish its vertical diameter. Their action is voluntary; and, by an effort of the will, it may be opposed more or less by the diaphragm, by which means the duration or intensity of the expiratory act is regulated. They are also attached to the ribs or costal cartilages, and, while they press the diaphragm upward, depress the ribs and thus diminish the antero-posterior and transverse diameters of the chest. In this action, they may be opposed by the voluntary contraction of the muscles which raise the ribs, also for the purpose of regulating the character of the expiratory act. The importance of this kind of action in declamation, singing, blowing, etc., is evident; and the skill exhibited by vocalists and performers on wind instruments shows how delicately this may be regulated by practice.

In labored respiration in disease and in the hurried respiration which follows violent exercise, the auxiliary muscles of expiration, as well as of inspiration, are called into action to a considerable extent.

Obliquus Externus.—This muscle, in connection with the obliquus internus and transversalis, is efficient in forced or labored expiration, by pressing the abdominal viscera against the diaphragm. Its fibres run obliquely from above downward and forward. Acting from its attachments to the linea alba, the crest of the ileum, and Poupart's ligament, by its attachment to the eight inferior ribs, it draws the ribs downward.

Obliquus Internus.—This muscle also acts in forced expiration, by compressing the abdominal viscera. The direction of its fibres is from below upward and forward. Acting from its attachments to the crest of the ileum, Poupart's ligament, and the lumbar fascia, by its attachments to the cartilages of the four inferior ribs, it draws them downward. The direction of the fibres of this muscle is the same as that of the internal intercostals. By its action the ribs are drawn inward as well as downward.

Transversalis.—The expiratory action of this muscle is mainly in compressing the abdominal viscera.

Sacro-lumbalis.—This muscle is situated at the posterior portion of the abdomen and thorax. Its fibres pass from its origin at the sacrum, upward and a little outward, to be inserted into the six inferior ribs at their angles. In expiration it draws the ribs downward, acting as an antagonist to the lower levatores costarum.

There are some other muscles which may be brought into action in forced expiration, assisting in the depression of the ribs, such as the serratus posticus inferior, the superior fibres of the serratus magnus, the inferior portion of the trapezius, but their function is unimportant.

Types of Respiration.—In the expansive movements of the chest, although all the muscles which have been classed as ordinary inspiratory muscles are brought into action to a greater or less extent, the fact that certain sets may act in a more marked manner than others has led physiologists to recognize different types of respiration. The three following types are generally given in works on physiology:

1. *The Abdominal type.*—In this, the action of the diaphragm and the consequent movements of the abdomen are most prominent.

2. *The Inferior Costal type.*—In this, the action of the muscles which expand the lower part of the thorax, from the seventh rib inclusive, is most prominent.

3. *The Superior Costal type.*—In this, the action of the muscles which dilate the thorax above the seventh rib and which elevate the entire chest is most prominent.

The abdominal type is most marked in children under the age of three years, irrespective of sex. In them, respiration is carried on almost exclusively by the diaphragm.

At a variable period after birth, a difference in the types of respiration in the sexes begins to show itself. In the male, the abdominal conjoined with the inferior costal type is predominant, and this continues through life. In the female, the inferior costal type is insignificant, and the superior costal type predominates. Observers differ in their statements of the period of life when this distinction in the sexes becomes apparent. Without discussing the nice question as to the exact age when this difference in the sexes first makes its appearance, it may be stated, in general terms, that, shortly before the age of puberty in the female, the superior costal type becomes more marked and soon predominates; while, in the male, respiration continues to be carried on mainly by the diaphragm and lower part of the chest.

The cause of the excessive movements of the upper part of the chest in the female has been the subject of considerable discussion. It is evident that it is not due to the mode of dress now so general in civilized countries, which confines the lower part of the chest and would render movements of expansion somewhat difficult, for the same phenomenon is observed in young girls and others who have never made use of such appliances. But there is evidently a physiological condition, the enlargement of the uterus in gestation, which, at certain times, would nearly arrest all respiratory movements, except those of the upper part of the chest. The peculiar mode of respiration in the female is a provision of Nature against the mechanical difficulties which would otherwise follow the physiological enlargement of the uterus. In pathology it is observed that, in consequence of this peculiarity, females are able to carry, without great inconvenience, immense quantities of water in the abdominal cavity; while a much smaller quantity, in the male, produces great distress from difficulty of breathing.

Frequency of the Respiratory Movements.—In counting the respiratory acts, it is desirable that the subject be unconscious of the observation, otherwise their normal character is apt to be disturbed. Of all who have written on this subject, Hutchinson presents the most numerous and convincing collection of facts. This observer ascertained the number of respiratory acts per minute, in the sitting posture, in 1,897 males. The results of his observations, with reference to frequency, are given in the following table:

Respirations per minute.	*Number of cases.*
From 9 to 16	79
16	239
17	105
18	195
19	74
20	561
21	129
22	143
23	42
24	243
24 to 40	87

Although this table shows considerable variation in different individuals, the great majority (1,731) breathed from sixteen to twenty-four times per minute. Nearly a third breathed twenty times per minute, a number which may be taken as the average.

The relations of the respiratory acts to the pulse are quite constant in health. It has been shown by Hutchinson that the proportion in the great majority of instances is one respiratory act to every four pulsations of the heart. The same proportion generally obtains when the pulse is accelerated in disease, except when the pulmonary organs are involved.

Age has an influence on the frequency of the respiratory acts, corresponding with what we have already noted with regard to the pulsations of the heart.

Quetelet gives the following as the results of observations on 300 males:

44 respirations per minute, soon after birth;
26, at the age of five years;
20, at the age of fifteen to twenty years;
19, at the age of twenty to twenty-five years;
16, about the thirtieth year;
18, from thirty to fifty years.

The influence of sex is not marked in very young children. The same observer noted no difference between males and females at birth; but in young women the respirations are a little less frequent than in young men of the same age.

The various physiological conditions which have been noted as affecting the pulse have a corresponding influence on respiration. In sleep, the number of respiratory acts is diminished by about twenty per cent. (Quetelet). Muscular effort accelerates the respiratory movements *pari passu* with the movements of the heart.

Relations of Inspiration and Expiration to each other—The Respiratory Sounds.—In ordinary respiration, inspiration is produced by the action of muscles, and expiration, in greatest part, by the passive reaction of the elastic walls of the thorax and the lungs. The inspiratory and expiratory acts do not immediately follow each other. Commencing with inspiration, it is found that this act maintains about the same intensity from its beginning to its termination; there is then a very brief interval, when expiration follows, which has its maximum of intensity at the commencement of the act and gradually dies away.[1] Between the acts of expiration and inspiration is an interval, which is somewhat longer than that which occurs after inspiration.

The duration of expiration is generally somewhat greater than that of inspiration, although they may be nearly, or in some instances quite equal. After from five to eight ordinary respiratory acts, an effort generally occurs which is rather more profound than the rest, and by which the air in the lungs is more effectually changed. The temporary arrest of the acts of respiration in violent muscular efforts, in straining, in parturition, etc., is familiar to all.

Ordinarily respiration is not accompanied by any sound which can be heard without applying the ear directly, or by the intervention of a stethoscope, to the respiratory organs; except when the mouth is closed and breathing is carried on exclusively through the nasal passages, when a soft, breezy murmur accompanies both acts. If the mouth be sufficiently opened to admit the free passage of air, no sound is to be heard in health. In sleep, the respirations are unusually profound; and, if the mouth be closed, the sound is rather more intense.

Snoring, a peculiar sound, more or less marked, which sometimes accompanies the respiratory acts during sleep, occurs when the air passes through both the mouth and the nose. It is more marked in inspiration, sometimes accompanying both acts, and sometimes it is not heard in expiration. It is not necessary to describe the characters of a sound so familiar. Snoring is an idiosyncrasy with many individuals, although those who do not snore habitually may do so when the system is unusually exhausted and relaxed. It only occurs when the mouth is open, and the sound is produced by vibration and a sort of flapping of the velum pendulum palati, between the two currents of air from the mouth and nose, together with a vibration in the column of air itself.

Applying the stethoscope over the larynx or trachea, a sound is heard, of a distinctly and purely tubular character, accompanying both acts of respiration. In inspiration, according to Dr. Austin Flint, "it attains its maximum of intensity quickly after the development of the sound and maintains the same intensity to the close of the act, when the sound abruptly ends, as if suddenly cut off." After a brief interval, the sound of ex-

[1] In listening to the respiratory murmur over the substance of the lungs, the expiratory follows the inspiratory sound without an interval. The interval between the acts of inspiration and expiration is only appreciated as the air passes in and out at the mouth.

piration follows. This is also tubular in quality; it soon attains its maximum of intensity, but, unlike the sound of inspiration, gradually dies away and is lost imperceptibly. It is seen that these phenomena correspond with the nature of the two acts of respiration.

Sounds approximating in character to the foregoing are heard over the bronchial tubes before they penetrate the lungs.

Over the substance of the lungs, a sound may be heard entirely different in its character from that heard over the larynx, trachea, or bronchial tubes. In inspiration, the sound is much less intense than over the trachea and has a breezy, expansive, or what is called in auscultation a vesicular character. It is much lower in pitch than the tracheal sound. It is continuous and rather increases in intensity from its commencement to its termination, ending abruptly, like the tracheal inspiratory sound. The sound is produced in part by the movement of air in the small bronchial tubes, but chiefly by the expansion of the innumerable air-cells of the lungs. It is followed, without an interval, by the sound of expiration, which is shorter, one-fifth to one-fourth as long, lower in pitch, and very much less intense. A sound is not always heard in expiration.

The variations in the intensity of the respiratory sounds in different individuals are very considerable. As a rule they are more intense in young persons; which has given rise to the term puerile respiration, when the sounds are exaggerated in parts of the lung, in certain cases of disease. The sounds are generally more intense in females than in males, particularly in the upper regions of the thorax.

It is difficult by any description or comparison to convey an accurate idea of the character of the sounds heard over the lungs and air-passages, and it is superfluous to make the attempt, when they can be so easily studied in the living subject.

Coughing, Sneezing, Sighing, Yawning, Laughing, Sobbing, and Hiccough.—These peculiar acts demand a few words of explanation. Coughing and sneezing are generally involuntary acts, produced by irritation in the air-tubes or nasal passages, although coughing is often voluntary. In both of these acts, there is first a deep inspiration, followed by a convulsive action of the expiratory muscles, by which the air is violently expelled with a characteristic sound, in the one case by the mouth, and in the other by the mouth and nares. Foreign bodies lodged in the air-passages are frequently expelled in violent fits of coughing. In hypersecretion of the bronchial mucous membrane, the accumulated mucus is carried by the act of coughing either to the mouth or well into the larynx, whence it is expelled by the act of expectoration. When either of these acts is the result of irritation from a foreign substance or secretions, it may be modified or partly smothered by the will, but is not completely under control. The exquisite sensibility of the mucous membrane at the summit of the air-passages, under most circumstances, protects them from the entrance of foreign matters, both liquid and solid; for the slightest impression received by the membrane gives rise to a violent and involuntary cough, by which the offending matter is removed. The glottis is also spasmodically contracted.

In sighing, a prolonged and deep inspiration is followed by a rapid and generally an audible expiration. This occurs, as a general rule, once in from five to eight respiratory acts, for the purpose of changing the air in the lungs more completely, and it is due to an exaggeration of the cause which gives rise to the ordinary acts of respiration. When due to depressing emotions, it has the same cause; for, at such times, respiration is less effectually performed. Yawning is an analogous process, but differs from sighing in the fact that it is involuntary and cannot be produced by an effort of the will. It is characterized by a wide opening of the mouth and a very profound inspiration. Yawning is generally assumed to be an evidence of fatigue, but it often occurs from a sort of contagion. When not the result of imitation, it has the same exciting cause as sighing, viz., deficient oxygenation of the blood, and it is followed by a sense of satisfaction, which shows that it meets some decided want on the part of the system.

Laughing and sobbing, though expressing opposite conditions, are produced by very much the same mechanism. The characteristic sounds accompanying these acts are the result of short, rapid, and convulsive movements of the diaphragm, accompanied by contractions of the muscles of the face, which produce the expressions characteristic of hilarity or grief. Although to a certain extent under the control of the will, these acts are mainly involuntary. Violent and convulsive laughter may be excited in many individuals by titillation of certain portions of the surface of the body. Laughter and sometimes sobbing, like yawning, may be the result of involuntary imitation.

Hiccough is a peculiar modification of the act of inspiration, to which it is exclusively confined. It is produced by a sudden, convulsive, and entirely involuntary contraction of the diaphragm, accompanied by a spasmodic constriction of the glottis. The contraction of the diaphragm is more extensive than in laughing and sobbing and occurs only once every four or five respiratory acts. The causes which give rise to hiccough are numerous, and many of them are referable to the digestive system. Among these may be mentioned the rapid ingestion of a quantity of dry food or of effervescing or alcoholic drinks. It occurs frequently in cases of disease.

Capacity of the Lungs, and the Quantity of Air changed in the Respiratory Acts.

Several points of considerable physiological interest arise in this connection. It is evident, from the simple experiment of opening the chest, when the elastic lungs collapse and expel a certain quantity of air which cannot be removed while the lungs are *in situ*, that a part of the gaseous contents of these organs necessarily remains after the most complete and forcible expiration. After an ordinary act, there is a certain quantity of air in the lungs which can be expelled by a forced expiration. In ordinary respiration, a comparatively small volume of air is introduced with inspiration, which is expelled by the succeeding expiration.[1] By the extreme action of all the inspiratory muscles in a forced inspiration, a supplemental quantity of air may be introduced into the lungs, which then contain much more than they ever do in ordinary respiration. For convenience, many physiologists have adopted the following names, which are applied to these various volumes of air:

1. *Residual Air;* that which is not and cannot be expelled by a forced expiration.
2. *Reserve Air;* that which remains after an ordinary expiration, deducting the residual air.
3. *Tidal, or ordinary Breathing Air;* that which is changed by the ordinary acts of inspiration and expiration.
4. *Complemental Air;* the excess over the ordinary breathing air, which may be introduced by a forcible inspiration.

The questions relating to the above divisions of the respired air have been made the subject of numerous investigations; but, although at first it might seem easy to determine all of them by a sufficient number of experiments, the necessary observations are attended with considerable difficulty, and the sources of error are numerous. In measuring the air changed in ordinary breathing, it has been found that the acts of respiration are so easily influenced by the mind and it is so difficult to experiment on any individual without his knowledge, that the results of many good observers are not to be relied upon. This is one of the most important of the questions under consideration. The difficulties in the way of estimating with accuracy the residual, reserve, or complemental volumes, will readily suggest themselves. The observations on these points, which may be taken as the most definite and exact, are those of Herbst, of Göttingen, and Hutchinson, of England. Those of the last-named observer are exceedingly elaborate and were

[1] Experiments have shown that a certain volume of air is lost in the lungs, the expired air being a little less in volume than the quantity inspired (from $\frac{1}{40}$ to $\frac{1}{50}$). This is not taken into account in this connection.

made on an immense number of subjects of both sexes and of all ages and occupations. They are generally accepted by physiologists as the most extended and accurate.

Residual Air.—Perhaps there is not one of the questions under consideration more difficult to answer definitely than that of the quantity of air which remains in the lungs after a forced expiration; but it fortunately is not one of any great practical importance. The residual air remains in the lungs as a physical necessity. The lungs are always, in health, in contact with the walls of the thorax; and, when this cavity is reduced to its smallest dimensions, it is impossible that any more air should be expelled. The volume which thus remains has been variously estimated at from forty cubic inches (Fontana) to two hundred and twenty cubic inches (Jurin). Dr. Hutchinson, who has carefully considered this point, estimates the residual volume at about one hundred cubic inches, but he states that it varies very considerably in different individuals. Taking every thing into consideration, we may assume this estimate to be as nearly correct as any. It is certain that the lungs of a man of ordinary size, at their minimum of distention, contain more than forty cubic inches of air; and, from measurements of the capacity of the thorax, deducting the estimated space occupied by the heart and vessels and the parenchyma of the lungs, it is shown that the residual air cannot amount to any thing like two hundred cubic inches.

There is no special division of the function of respiration connected with the residual air. It remains in the lungs merely as a physical necessity, and its volume must not be taken into account in considering the volumes which are changed in any of the operations connected with breathing.

Reserve Air.—This name is appropriately given to the volume of air which may be expelled and changed by a voluntary effort, but which remains in the lungs, added to the residual air, after an ordinary act of expiration. It may be estimated, without any reference to the residual air, by forcibly expelling air from the lungs, after an ordinary expiration. The average volume is one hundred cubic inches.

The reserve air is more or less changed whenever we experience a necessity for a more complete renovation of the contents of the lungs than ordinary. It is encroached upon in the unusually profound inspiration and expiration which occur every five or six acts. It is used in certain prolonged vocal efforts, in blowing, etc. Added to the residual air, it constitutes the minimum capacity of the lungs in ordinary respiration. As it is continually receiving watery vapor and carbonic acid, it is always more or less vitiated, and, when reënforced by the breathing air, which enters with inspiration, is continually in circulation, in obedience to the law of the diffusion of gases. Those who are in the habit of arresting respiration for a time, as pearl-divers, learn to change the reserve air as completely as possible by several forcible acts and then fill the lungs with fresh air. In this way they are enabled to suspend the respiratory acts for from one to two minutes without inconvenience. The introduction of fresh air with each inspiration, and the constant diffusion which is going on and by which the proper quantity of oxygen finds its way to the air-cells, give, in ordinary breathing, a composition to the air in the deepest portions of the lungs which insures a constant aëration of the blood.

Tidal, or Ordinary Breathing Air.—The volume of air which is changed in the ordinary acts of respiration is subject to immense physiological variations, and the respiratory movements, as regards intensity, are so easily influenced by the mind, that great care is necessary to avoid error in estimating the volume of ordinary breathing air. The estimates of Herbst and of Hutchinson are the results of very extended observations made with great care and are generally acknowledged to be as nearly accurate as possible. As a mean of these observations, it has been found that the average volume of breathing air, in a man of ordinary stature, is twenty cubic inches. According to Hutchinson, in perfect repose, when the respiratory movements are hardly perceptible, not more than from seven to twelve cubic inches are changed; while, under excitement, he has seen the volume increased to seventy-seven cubic inches. Of course the latter is temporary. Herbst noted that the breathing volume is constantly increased in proportion to the stature of the individual and bears no definite relation to the apparent capacity of the chest.

Complemental Air.—The thorax may be so enlarged by an extreme voluntary inspiratory effort as to contain a quantity of air much larger than after an ordinary inspiration. The additional volume of air thus taken in may be estimated by measuring all the air which can be expelled from the lungs after the most profound inspiration, and deducting the sum of the reserve air and breathing air. This quantity has been found by Hutchinson to vary in different individuals, bearing a close relation to stature. The mean complemental volume is one hundred and ten cubic inches.

The complemental air is drawn upon whenever an effort is made which requires a temporary arrest of respiration. Brief and violent muscular exertion is generally preceded by a profound inspiration. In sleep, as the volume of breathing air is somewhat increased, the complemental air is encroached upon. A part or the whole of the complemental air is also used in certain vocal efforts, in blowing, in yawning, in the deep inspiration which precedes sneezing, in straining, etc.

Summary.—In a healthy male of medium stature, the residual air, which cannot be expelled from the lungs, amounts to about one hundred cubic inches.

The reserve air, which can be expelled but which is not changed in ordinary respiration, amounts to about one hundred cubic inches.

The tidal air, which is changed in ordinary respiration, amounts to about twenty cubic inches.

The complemental air, which may be taken into the lungs after the completion of an ordinary act of inspiration, amounts to about one hundred and ten cubic inches.

Extreme Breathing Capacity.—By the extreme breathing capacity is meant the volume of air which can be expelled from the lungs by the most forcible expiration, after the most profound inspiration. This has been called by Dr. Hutchinson the vital capacity, as signifying "the volume of air which can be displaced by living movements." Its volume is equal to the sum of the reserve air, the breathing air, and the complemental air, and represents the extreme capacity of the chest, deducting the residual air. Its physiological interest is due to the fact that it can readily be determined by an appropriate apparatus, the spirometer, and comparisons can thus be made between different individuals, both healthy and diseased. The number of observations on this point made by Dr. Hutchinson is enormous, amounting in all to little short of five thousand.

The extreme breathing capacity in health is subject to variations which have been shown to bear a very close relation to the stature of the individual. Hutchinson commences with the proposition that, in a man of medium height (five feet eight inches), it is equal to two hundred and thirty cubic inches. He has shown that the extreme breathing capacity is constant in the same individual, and that it is not to be increased by habit or practice.

The most striking result of the experiments of Dr. Hutchinson, with regard to the modifications of the vital capacity, is that it bears a definite relation to stature, without being affected in a very marked degree by weight or the circumference of the chest. This is especially remarkable, as it is well known that height does not depend so much upon the length of the body as upon the length of the lower extremities.

It has been ascertained that for every inch in height, between five and six feet, the extreme breathing capacity is increased eight cubic inches.

The following table shows the mean results of the immense number of observations on which this conclusion is based:

Progression of the Vital Capacity Volume with the Stature.

Height.		Series from observations on 1,012 cases.	Series from observations on 1,923 cases.	Series in arithmetical progression.
		1st result.	2d result.	
5 feet 0 inches / 5 " 2 "	5 feet 1 inch...........	175·0	176·0	174·0
5 " 2 " / 5 " 4 "	5 " 3 "	188·5	191·0	190·0
5 " 4 " / 5 " 6 "	5 " 5 "	206·0	207·0	206·0
5 " 6 " / 5 " 8 "	5 " 7 "	222·0	228·0	222·0
5 " 8 " / 5 " 10 "	5 " 9 "	237·5	241·0	238·0
5 " 10 " / 6 " 0 "	5 " 11 "	254·5	258·0	254·0
Mean of all Heights......................		214·0	217·0	214·0

Age has an influence, though less marked than stature, upon the extreme breathing capacity. As the result of 4,800 observations (males), it was ascertained that the volume increases with age up to the thirtieth year, and progressively decreases, with tolerable regularity, from the thirtieth to the sixtieth year. These figures, though necessarily subject to certain individual variations, may be taken as the basis for examinations of the extreme breathing capacity in disease, which frequently give important information. Of course, the breathing capacity is modified by any abnormal condition which interferes with the mobility of the thorax or the dilatability of the lungs.

Relations in Volume of the Expired to the Inspired Air.—A certain proportion of the inspired air is lost in respiration, so that the air expired is always a little less in volume than that which is taken into the lungs. All the older experimenters, except Magendie, were agreed upon this point. The loss was put by Davy at $\frac{1}{70}$, and by Cuvier at $\frac{1}{50}$ of the amount of air introduced. Observations on this point, to be exact, must include a considerable number of respiratory acts; and, from the difficulty of continuing respiration in a perfectly regular and normal manner when the attention is directed to that function, the most accurate results may probably be obtained from experiments on the lower animals. Despretz caused six young rabbits to respire for two hours in a confined space containing two hundred and ninety-nine cubic inches of air, and ascertained that the volume had diminished sixty-one cubic inches, or a little more than one-fiftieth. We may take the approximations of Davy and Cuvier, as applied to the human subject, as nearly correct, and assume that, in the lungs, from $\frac{1}{70}$ to $\frac{1}{50}$ of the inspired air is lost.

Diffusion of Air in the Lungs.—When it is considered that, with each inspiration, but about twenty cubic inches of fresh air is introduced, sufficient only to fill the trachea and larger bronchial tubes, it is evident that some forces must act by which this fresh air finds its way into the air-cells and the vitiated air is brought into the larger tubes, to be expelled with the succeeding expiration. The expired air may become so charged with noxious gases, by holding the breath for a few seconds, that, when collected in a receiver under water, it is incapable of supporting combustion.

The interchange between the fresh air in the upper portions of the respiratory apparatus and the air in the deeper parts of the lungs is constantly going on, in obedience to the well-known law of the diffusion of gases, aided by the active currents or impulses produced by the alternate movements of the chest. When two gases, or mixtures of gases, of different densities are brought in contact with each other, they diffuse or mingle with great rapidity, until, if undisturbed, the whole mass has a uniform density and composition. This has been shown to take place between very light and very heavy gases in opposition to the laws of gravity, and even when two reservoirs are connected by a small tube many feet in length, though then it proceeds quite slowly. In the respiratory apparatus, at the termination of inspiration, the atmospheric air, composed of a mixture of oxygen and nitrogen, is introduced into the tubes with a considerable impetus and is brought into contact with the gas in the lungs, which is much heavier, as it contains a considerable quantity of carbonic acid. Diffusion then takes place, aided by the elastic lungs, which are gradually forcing the gaseous contents out of the cells, until a certain portion of the air loaded with carbonic acid finds its way to the larger tubes, to be thrown off in expiration, its place being supplied by the fresh air.

In obedience to the law established by Graham, that the diffusibility of gases is inversely proportionate to the square root of their densities, the penetration of atmospheric air, which is the lighter gas, to the deep portions of the lungs would take place with greater rapidity than the ascent of the air charged with carbonic acid; so that eighty-one parts of carbonic acid should be replaced by ninety-five of oxygen. It is found, indeed, that the volume of carbonic acid exhaled is always less than the volume of oxygen absorbed. This diffusion is constantly going on, so that the air in the pulmonary vesicles, where the interchange of gases with the blood takes place, maintains a pretty uniform composition. The process of aëration of the blood, therefore, has none of that intermittent character which attends the muscular movements of respiration, which would undoubtedly occur if the entire gaseous contents of the lungs were changed with every respiratory act.

CHAPTER V.

CHANGES WHICH THE AIR AND THE BLOOD UNDERGO IN RESPIRATION.

Composition of the air—Consumption of oxygen—Exhalation of carbonic acid—Influence of age—Relations between the quantity of oxygen consumed and the quantity of carbonic acid exhaled—Exhalation of watery vapor—Exhalation of ammonia—Exhalation of organic matter—Exhalation of nitrogen—Changes of the blood in respiration (hæmatosis)—Difference in color between arterial and venous blood—Comparison of the gases in venous and arterial blood—Analysis of the blood for gases—Relative quantities of oxygen and carbonic acid in venous and arterial blood—Nitrogen of the blood—Condition of the gases in the blood—Mechanism of the interchange of gases between the blood and the air in the lungs—Relations of respiration to nutrition, etc.—Views of physiologists anterior to the time of Lavoisier—Relations of the consumption of oxygen to nutrition—Relations of the exhalation of carbonic acid to nutrition—Essential processes of respiration—The respiratory sense, or want on the part of the system which induces the respiratory movements—Respiratory efforts before birth—Cutaneous respiration—Asphyxia.

From the allusions which we have already made to the general process of respiration, it is apparent that, before the discovery of the nature of the gases which compose the air and those which are exhaled from the lungs, it was impossible for physiologists to have any correct ideas of the nature of this important function. It is not surprising that the ancients, observing the regular introduction of air into the lungs and noting the fact that the air is generally much cooler than the body, supposed the great object of respiration to be the cooling of the blood. It is also evident that no definite knowledge of any of the processes of respiration could exist prior to the discovery of the circulation of the blood and our knowledge of the composition of the air and the properties of oxygen.

The discovery of the properties of oxygen and carbonic acid, although bearing upon the great question under consideration, were simply isolated facts and failed to develop any definite idea of the changes of the air and blood in respiration. The application of these facts was made by the great chemist, Lavoisier, who was the first to employ the delicate balance in chemical investigation, and whose observations mark the beginning of an accurate knowledge of the function of respiration. With the balance, Lavoisier showed the nature of the oxides of the metals; he discovered that carbonic acid is formed by a union of carbon and oxygen; and, noting the consumption of oxygen and the production of carbonic acid in respiration, advanced, for the first time, the view that the one was employed in the production of the other. Although, as would naturally be expected, the doctrines of this great observer have been modified with the advances in science, he developed facts which will stand forever, and which have served as the starting-point of all our knowledge on this subject. From that time, physiologists began to regard respiration as consisting in the appropriation of oxygen and the exhalation of carbonic acid; and now the seat of this process is simply changed from the lungs to the tissues. From the limited knowledge of the intimate phenomena of nutrition which obtained in his day, Lavoisier could not be expected to entertain any other view than that the carbonic acid produced was the result of a direct union of oxygen with carbon in the blood. It is only since investigations have made manifest the great complexity of the processes of nutrition, that some are unwilling to believe that carbonic acid is produced in so simple a way as it appeared to Lavoisier.

Composition of the Air.—Pure atmospheric air is a mechanical mixture of 79·19 parts of nitrogen with 20·81 parts of oxygen (Dumas and Boussingault). It contains, in addition, a very small quantity of carbonic acid, about one part in 2,000 by volume. The air is never free from moisture, which is very variable in quantity, being generally more abundant at a high than at a low temperature. In 1840, Schönbein discovered in the air a peculiarly odorous principle called ozone, which he conceived to be a compound of oxygen and hydrogen, but which is now pretty well shown to be an allotropic form of oxygen. Oxygen obtained by decomposing water by the Voltaic pile is in this condition. It exists in very small quantity in the air, and, as far as we know, plays no important part in the function of respiration. Its chief interest has been in its theoretical relations to epidemic diseases. Floating in the atmosphere, are a number of excessively-minute organic bodies. Various odorous and other gaseous matters may be present as accidental constituents of the atmosphere.

In considering the function of respiration, it is not necessary to take account of any of the constituents of the atmosphere except oxygen and nitrogen, the others being either inconstant or existing in excessively minute quantity. It is necessary to the regular performance of the function, that the air should contain about four parts of nitrogen to one of oxygen and have about the density which exists on the general surface of the globe. When the density is very much increased, as in mines, respiration is usually more or less disturbed. By exposure to a rarefied atmosphere, as in the ascent of high mountains or in aërial voyages, respiration may be very seriously interfered with, from the fact that less oxygen than usual is presented to the respiratory surface and the reduced atmospheric pressure diminishes the capacity of the blood for holding gases in solution.

Magendie and Bernard, in experimenting on the minimum proportion of oxygen in the air which is capable of sustaining life, found that a rabbit, confined under a bell-glass, with an arrangement for removing the carbonic acid and water exhaled as fast as they were produced, died of asphyxia when the quantity of oxygen became reduced to from three to five per cent.

A few experiments are on record in which the human subject and animals have been made to respire for a time pure oxygen. Although this is the gas which is essential in ordinary respiration, the process being carried on about as well in a mixture of oxygen with hydrogen as with nitrogen, the functions do not seem to be much altered when the pure gas is taken into the lungs. Allen and Pepys confined animals for twenty-four hours in an atmosphere of pure oxygen without any notable results; but, as is justly remarked by Longet, these experiments do not show that it would be possible to respire unmixed oxygen indefinitely without inconvenience. As it exists in the air, oxygen is undoubtedly in the best form for the permanent maintenance of the respiratory function. The blood seems to have a certain capacity for the absorption of oxygen, which is not increased when the pure gas is respired.

The only other gas which has the power of maintaining respiration, even for a time, is nitrous oxide. This is absorbed by the blood-corpuscles with great avidity, and, for a time, it produces an exaggeration of the vital processes, with delirium, etc.—properties which have given it the common name of the laughing gas; but this condition is followed by anæsthesia, and finally asphyxia, probably because the gas has such an affinity for the blood-corpuscles as to remain to a certain extent fixed, interfering with that interchange of gases which is essential to life. Notwithstanding this, experimenters have confined with impunity rabbits and other animals in an atmosphere of nitrous oxide for a number of hours. In all cases they became asphyxiated, but in some instances were restored on being brought again into the ordinary atmosphere.

Other gases which may be introduced into the lungs either produce asphyxia, negatively, from the fact they are not absorbed by the blood and are incapable of carrying on respiration, like hydrogen or nitrogen, or positively, by a poisonous effect on the system. The most important of the gases which act as poisons are, carbonic oxide, sulphuretted hydrogen, and arseniuretted hydrogen. It is somewhat uncertain whether carbonic acid exert its deleterious influence as a poison or as merely taking the place of the oxygen in the blood-corpuscles. It is easily displaced from the blood by oxygen, and therefore does not seem to possess the properties of a poison, like carbonic oxide and some other gases, which become fixed in the blood and are not readily displaced when fresh air is introduced into the lungs.

Consumption of Oxygen.—The determination of the quantity of oxygen which is removed from the air by the process of respiration is a question of great physiological interest and one which engaged largely the attention of Lavoisier and those who have followed in his line of observation. On this point, there is an accumulated mass of observations, which are comparatively unimportant from the fact that they were made before the means of analysis of the gases were as perfect as they now are. Although many of the results obtained by the older experimenters are interesting and instructive as showing the comparative quantities of oxygen consumed under various physiological conditions, they are not to be compared with the more recent observations. In the observations of Regnault and Reiset, the animal to be experimented upon was enclosed in a receiver filled with air, a measured quantity of oxygen was introduced as fast as it was consumed by respiration, and the carbonic acid was constantly removed and carefully estimated. In most of the experiments, the confinement did not appear to interfere with the functions of the animal, which ate and drank in the apparatus and was in as good condition at the termination as at the beginning of the observation. This method is much more accurate than that of simply causing an animal to breathe in a confined space, when the consumption of oxygen and accumulation of carbonic acid and other matters must interfere more or less with the proper performance of the respiratory function. As employed by Regnault and Reiset, it is only adapted to experiments on animals of small size. These give but an approximate idea of the processes as they take place in the human subject, as it is natural to suppose that the relative quantities of gases consumed and produced in respiration vary in different orders of animals.

In the researches on respiration by Dr. Max Pettenkofer, the conditions for accurate observation on the human subject seem to have been fulfilled. Dr. Pettenkofer constructed a chamber large enough to admit a man and allow perfect freedom of motion, eating, sleeping, etc., into which air could be constantly introduced in definite quantity, and from which the products of respiration were constantly removed and estimated. An incomplete series of observations is published, which has particular reference to the products of respiration; and, thus far, the subject of consumption of oxygen has not been fully considered. This method was adapted to the human subject on a small scale in 1843, by Scharling, but there was no arrangement for estimating the quantity of oxygen furnished.

Estimates of the absolute quantities of oxygen consumed, or of carbonic acid exhaled, based on analyses of the inspired and expired air, calculations from the average quantity of air changed with each respiratory act, and the average number of respirations per minute, are by no means so reliable as analyses showing the actual changes in the air, like those of Regnault and Reiset, provided the physiological conditions be fulfilled. When there is so much multiplication and calculation, a very slight and perhaps unavoidable inaccuracy in the quantities consumed or produced in a single respiration will make an immense error in the estimate for a day or even an hour. Bearing in mind all these sources of error, from the experiments of Valentin and Brunner, Dumas, Regnault and Reiset, and others, a sufficiently-accurate approximation of the proportion of oxygen consumed by the human subject may be formed. The air, which contains, when inspired, 20·81 parts of oxygen per 100, is found on expiration to contain but about 16 parts per 100. In other words, the volume of oxygen absorbed in the lungs is five per cent. or $\frac{1}{20}$ of the volume of air inspired. It is interesting and useful to extend this estimate as far as possible to the quantity of oxygen absorbed in a definite time; for the regulation of the supply of oxygen where many persons are assembled, as in public buildings, hospitals, etc., is a question of great practical importance. Assuming that the average respirations per minute are eighteen, and that, with each act, twenty cubic inches of air are changed, fifteen cubic feet of oxygen are consumed in the twenty-four hours, which represent three hundred cubic feet of pure air. This is the minimum quantity of air which is actually used, making no allowance for any increase in the intensity of the respiratory processes, which is liable to occur from various causes. To meet all the respiratory exigencies of the system, in hospitals, prisons, etc., it has been found necessary to allow at least eight hundred cubic feet of air for each person, unless the situation be such that the air is changed with unusual frequency; for, beside the actual loss of oxygen in the respired air, constant emanations from both the pulmonary and cutaneous surfaces are taking place, which should be removed. In some institutions as much as twenty-five hundred cubic feet of air is allowed to each person.

The quantity of oxygen consumed is subject to great variations, depending upon temperature, the condition of the digestive system, muscular activity, etc. The following conclusions, the results of the observations of Lavoisier and Séguin, give at a glance the variations from the above-mentioned causes:

"1. A man, in repose and fasting, with an external temperature of 90° Fahr., consumes 1,465 cubic inches of oxygen per hour.

"2. A man, in repose and fasting, with an external temperature of 59° Fahr., consumes 1,627 cubic inches of oxygen per hour.

"3. A man, during digestion, consumes 2,300 cubic inches of oxygen per hour.

"4. A man, fasting, while he accomplishes the labor necessary to raise, in fifteen minutes, a weight of 7,343 kil. (about 16 lb. 3 oz. av.) to the height of 656 feet, consumes 3,874 cubic inches of oxygen per hour.

"5. A man, during digestion, accomplishing the labor necessary to raise, in fifteen minutes, a weight of 7,343 kil. (about 16 lb. 3 oz. av.) to the height of 700 feet, consumes 5,568 cubic inches of oxygen per hour."

All who have experimented on the influence of temperature upon the consumption of oxygen, in the warm-blooded animals and in the human subject, have noted a marked increase at low temperatures. Immediately after birth, the consumption of oxygen in the warm-blooded animals is relatively very slight. Buffon and Legallois have shown that, just after birth, dogs and other animals will live for half an hour or more under water; and cases are on record where life has been restored in newly-born children after seven, and, it has been stated, after twenty-three hours of asphyxia. (Milne-Edwards.) During the first periods of existence, the condition of the newly-born approximates to that of a cold-blooded animal. The lungs are relatively very small, and it is some time before they fully assume their function. The muscular movements are hardly more than is necessary to take the small amount of nourishment consumed at that period, and nearly all of the time is passed in sleep. There is also very little power of resistance to low temperature. Although accurate researches regarding the comparative quantities of oxygen in the venous and arterial blood of the fœtus are wanting, it has been frequently observed that the difference in color is not so marked as it is after pulmonory respiration becomes established. The direct researches of W. F. Edwards have shown that the absolute consumption of oxygen by very young animals is very small; and the observations of Legallois on rabbits, made every five days during the first month of existence, show a rapidly-increasing demand for this principle with age.

Regnault and Reiset have shown that the consumption of oxygen is greater in lean than in very fat animals, provided they be in perfect health. They have also shown that the consumption is much greater in carnivorous than in herbivorous animals; and, in animals of different sizes, it is relatively much greater in those which are very small. In small birds, such as the sparrow, the relative quantity of oxygen absorbed was ten times greater than in the fowl.

During sleep the quantity of oxygen consumed is considerably diminished; and in hibernation it is so small, that Spallanzani could not detect any difference in the composition of the air in which a marmot, in a state of torpor, had remained for three hours. In experiments on a marmot in hibernation, Regnault and Reiset observed a reduction in the quantity of oxygen consumed to about $\frac{1}{30}$ of the normal standard.

It has been shown by experiments, that the consumption of oxygen bears a pretty constant ratio to the production of carbonic acid; and, as the observations upon the influence of sex, number of respiratory acts, etc., on the activity of the respiratory processes, have been made chiefly with reference to the carbonic acid exhaled, we shall consider these influences in connection with the products of respiration.

Experiments on the effect of increasing the proportion of oxygen in the air have led to varied results in the hands of different observers. Regnault and Reiset, whose observations on this point are generally accepted, did not discover any increase in the consumption of oxygen when this gas was largely in excess in the atmosphere.

The results of confining an animal in an atmosphere composed of twenty-one parts of oxygen and seventy-nine parts of hydrogen are very curious and instructive. When hydrogen is thus substituted for the nitrogen of the air, the consumption of oxygen is largely increased. Regnault and Reiset attribute this to the superior refrigerating power of the hydrogen; but a more rational explanation would seem to be in its superior diffusibility. Hydrogen is the most diffusible of all gases; and, when introduced into the lungs in place of the nitrogen of the air, the vitiated air, charged with carbonic acid, is undoubtedly more readily removed from the deep portions of the lungs, giving place to the mixture of hydrogen and oxygen. It is probably for this reason that the quantity of oxygen consumed is increased. It is probable that the nitrogen of the air plays an important part in the phenomena of respiration by virtue of its degree of diffusibility.

In view of the great variations in the consumption of oxygen dependent on different physiological conditions, such as digestion, exercise, temperature, etc., it is impossible to fix upon any number which will represent, even approximatively, the average quantity consumed per hour. The estimate arrived at by Longet, from a comparison of the results obtained by different reliable observers, is perhaps as near the truth as possible. This estimate puts the hourly consumption at from 1,220 to 1,525 cubic inches, "in an adult male, during repose and in normal conditions of health and temperature."

In passing through the lungs, the air, beside losing a proportion of its oxygen, undergoes the following changes:

1. Increase in temperature.
2. Gain of carbonic acid.
3. Gain of watery vapor.
4. Gain of ammonia.
5. Gain of a small quantity of organic matter.
6. Gain, and occasionally loss, of nitrogen.

The elevation in temperature of the air which has passed through the lungs has been carefully observed by Dr. Gréhant. He found that, with an external temperature of 72° Fahr., respiring seventeen times per minute, the air taken in by the nares and expired by the mouth, through an apparatus containing a thermometer carefully protected from external influences, marked a temperature of 95·4°. Taking in the air by the mouth, the temperature of the expired air was 93°. At the commencement of the expiration, Dr. Gréhant noted a temperature of 94°. After a prolonged expiration, the temperature was 96°. In these observations, the temperature taken beneath the tongue was 98°.

Exhalation of Carbonic Acid.—The production of carbonic acid in the respiratory process is as universal as the consumption of oxygen. Experiments have shown that all animals during life exhale this principle, as well as all tissues, so long as they retain their irritability. This takes place, not only when the animals or tissues are placed in an atmosphere of oxygen or common air, but, as was observed by Spallanzani, in an atmosphere of pure nitrogen or hydrogen. This fact has since been noted by W. F. Edwards, J. Müller, G. Liebig, Bert, and others.

The study of the exhalation of carbonic acid presents several problems of great physiological interest:

1. What is the absolute quantity of carbonic acid exhaled by the lungs in a given time?

2. What are the variations in the exhalation of this principle due to physiological influences?

3. What is the relation between the quantity of carbonic acid produced and the quantity of oxygen consumed?

On account of the variations in the quantities of carbonic acid exhaled at different periods of the day, and particularly the great influence of the rapidity of the respiratory movements, it is exceedingly difficult to fix upon any number that will represent the average proportion of this gas contained in the expired air. The same influences were found affecting the consumption of oxygen, and the same difficulties were experienced in forming an estimate of the proportion of this gas consumed. As we assumed, after a comparison of the results obtained by different observers, that the volume of oxygen consumed is about five per cent. of the entire volume of air, it may be stated, as an approximation, that, in the intervals of digestion, in repose, and under normal conditions as regards the frequency of the pulse and respiration, the volume of carbonic acid exhaled is about four per cent. of the volume of the expired air. As the volume of oxygen which enters into the composition of a definite quantity of carbonic acid is precisely equal to the volume of the carbonic acid, it is seen that a certain quantity of oxygen disappears in respiration and is not represented in the carbonic acid exhaled.

There are great differences in the proportion of carbonic acid in the expired air, depending upon the time during which the air has remained in the lungs. This interesting point has been studied by Vierordt, in a series of ninety-four experiments made upon his own person, with the following results:

"When the respirations are frequent, the quantity of carbonic acid expelled at each expiration is much less than in a slow expiration; but the quantity of carbonic acid produced during a given time by frequent respirations is greater than that which is thrown off by slow expirations."

The air which escapes during the first period of an expiration is naturally less rich in carbonic acid than that which is last expelled and comes directly from the deeper portions of the lungs. Dividing, as nearly as possible, the expiration into two equal parts, Vierordt found, as the mean of twenty-one experiments, a percentage of 3·72 in the first part of the expiration and 5·44 in the second part.

Temporary arrest of the respiratory movements, as we should expect, has a marked influence in increasing the proportion of carbonic acid in the expired air; although the absolute quantity exhaled in a given time is diminished. In a number of experiments on his own person, Vierordt ascertained that the percentage of carbonic acid becomes uniform in all parts of the respiratory organs, after holding the breath for forty seconds. Holding the breath after an ordinary inspiration, for twenty seconds, the percentage of carbonic acid in the expired air was increased 1·73 over the normal standard; but the absolute quantity exhaled was diminished by 2·642 cubic inches. After taking the deepest possible inspiration and holding the breath for one hundred seconds, the percentage was increased 3·08 above the normal standard; but the absolute quantity was diminished more than fourteen cubic inches. Allen and Pepys state that air which has passed nine or ten times through the lungs contains 9·5 per cent. of carbonic acid.

Vierordt gives the following formula as representing the influence of the frequency of the respirations on the production of carbonic acid: Taking 2·5 parts per hundred as representing the constant value of the gas exhaled by the blood, the increase over this proportion in the expired air is in exact ratio to the duration of the contact of the air and blood.

The absolute quantity of carbonic acid exhaled in a given time is a more important subject of inquiry than the proportion contained in the expired air; for the latter is constantly varying with every modification in the number and extent of the respiratory acts, and the volume of breathing air is subject to great fluctuations and is very difficult of determination.

Among the most reliable observations on the quantity of carbonic acid exhaled by the human subject in a definite time and the variations to which it is subject, are those of Andral and Gavarret and of Dr. Edward Smith. The observations of Lavoisier and Séguin, Prout, Davy, Dumas, Allen and Pepys, Scharling, and others, have none of them seemed to fulfil the necessary experimental conditions so completely. Scharling's method was to enclose his subject in a tight box, with a capacity of about twenty-seven cubic feet, to which air was constantly supplied; but the observations were comparatively few, being made on only six persons. In his observations, the quantities of gas exhaled must have been considerably modified by the elevation of temperature and exhalation of moisture in so small a space. The mental condition of the subject of an experiment has an influence upon the products of respiration, and the function is sometimes modified from the mere fact that an experiment is being performed; an influence which Scharling did not fail to recognize, but which frequently cannot be guarded against.

The observations of Andral and Gavarret were made on sixty-two persons of both sexes and different ages and under absolutely identical conditions as regards digestion, time of the day, barometric pressure, and temperature. The products of respiration were collected in the following way: A thin mask of copper covering the face and large enough to contain an entire expiration was fitted to the face by its edges, which were provided with India-rubber so as to make it air-tight. At the upper part was a plate of glass for the admission of light, and at the lower part, an opening, which allowed the entrance of air but was provided with a valve preventing its escape. By another opening, the mask was connected by a rubber tube with three glass balloons, capable of holding 8,544 cubic inches, in which a vacuum had been previously established. With the mask fixed upon the face, and a stopcock opened, connected with the balloons, so as to graduate the current of air, the subject respires freely in the current which comes from the exterior into the receivers. In this way, although the quantity of air respired is not measured, the vacuum in the receivers draws in the products of respiration. The current will continue for from eight to thirteen minutes and is so regulated that the air is respired but once. The quantity of carbonic acid in the receivers represents the quantity produced during the time that the experiment has been going on. By carefully fulfilling all the physiological conditions, regulating the number of respirations, as far as possible, to the normal standard, different observations on the same subject, at different times and under the same conditions, were attended with results so nearly identical as to give every confidence in the accuracy of the process. But even then, these observers recognized such immense variations in the exhalation of carbonic acid with the constantly-varying physiological conditions, that they did not feel justified in taking their observations as a basis for calculations of the entire quantity exhaled in the twenty-four hours.

The results of the above-mentioned observations on the male, between the ages of sixteen and thirty, between 1 and 2 P. M., under identical conditions of the digestive and muscular systems, each experiment lasting from eight to thirteen minutes, showed an exhalation of about 1,220 cubic inches of carbonic acid per hour.

Dr. Edward Smith, in his elaborate paper on the phenomena of respiration, employed a very rigorous method for the estimation of the carbonic acid exhaled. He used a mask, fitting closely to the face, which covered only the air-passages. The air was admitted after being measured by passing through an ordinary dry gas-meter. The expired air was passed through a drying apparatus, and the carbonic acid was absorbed by a solution of potash, arranged in a number of layers so as to present a surface of about seven hundred square inches, and carefully weighed. This apparatus was capable of collecting all the carbonic acid exhaled in an hour. The estimate was made for eighteen waking hours and six hours of sleep. The observations for the eighteen hours were made on four persons; namely, Dr. Smith, æt. 38 years, weighing 196 pounds, 6 feet high, with a vital capacity of 280 cubic inches; Mr. Moul, æt. 48 years, 5 feet 9½ inches high, 175 pounds weight; Dr. Murie, æt. 26 years, 5 feet 7½ inches high, 133 pounds weight, vital capacity 250 cubic inches; Prof. Frankland, æt. 33 years, 5 feet 10½ inches high, and 136 pounds weight. Breakfast was taken at 8½ A. M., dinner at 1½, tea at 5½, and supper at 8½ P. M. The observations occupied ten minutes and were made every hour and half-hour for eighteen hours. The average for the eighteen hours gave 20,082 cubic inches of carbonic acid for the whole period. Observations during the six hours of sleep showed a total exhalation of 4,126 cubic inches. This, added to the quantity exhaled during the day, gives as the total exhalation in the twenty-four hours, during complete repose, 24,208 cubic inches (about 14·24 cubic feet), containing 7·144 oz. av. of carbon. Considering the great variations in the exhalation of carbonic acid, this estimate can be nothing more than an approximation. One of the great modifying influences is muscular exertion, by which the production of carbonic acid is largely increased. This would indicate a larger quantity during ordinary conditions of exercise, and a much larger quantity in the laboring classes. Dr. Smith gives the following approximate estimates of these differences:

In quietude	7·144 oz. av. of carbon.
Non-laborious class	8·68 " "
Laborious class	11·7 " "

In studying the variations in the exhalation of carbonic acid, important information has been derived from experiments by many observers on the inferior animals, as well as from the observations of Dumas, Prout, Scharling, Pettenkofer, and others, on the human subject. The principal conditions which influence the exhalation of this principle are the following: Age and sex; activity or repose of the digestive system; form of diet; sleep; muscular activity; fatigue; moisture and surrounding temperature; season of the year.

Influence of Age.—In treating of the consumption of oxygen, it was stated that, during the first few days of extra-uterine existence, the demand for oxygen on the part of the system is very slight. At this period there is a correspondingly-feeble exhalation of carbonic acid. It is well known that, during the first hours and days after birth, the new being has little power of generating heat, needs constant protection from changes in temperature, and the voluntary movements are very imperfect. During the first few days, indeed, the infant does little more than sleep and take the small quantity of colostrum which is furnished by the mammary glands of the mother. While the animal functions are so imperfectly developed and until the nourishment becomes more abundant and the child begins to increase rapidly in weight, the quantity of carbonic acid exhaled is very small.

After the respiratory function has become fully established, it is probable, from the greater number of respiratory movements in early life, that the production of carbonic acid, in proportion to the weight of the body, is greater in infancy than in adult life. Direct observations, however, are wanting on this point.

The observations of Andral and Gavarret show the comparative exhalation of carbonic acid in the male, from the age of twelve to eighty-two, and give the results of a single observation at the age of one hundred and two years. They show an increase in the absolute quantity exhaled, from the age of twelve to thirty-two; a slight diminution, from thirty-two to sixty; and a considerable diminution, from sixty to eighty-two. These results are given in the following table:

	Carbonic acid exhaled per hour
In boys from twelve to sixteen years..........................	915 cubic inches.
In young men from seventeen to nineteen years...............	1,220 " "
In men from twenty-five to thirty-two years..................	1,343 " "
In men from thirty-two to sixty years.........................	1,220 " "
In men from sixty-three to eighty-two years..................	933 " "
In an old man of one hundred and two years..................	671 " "

Taking into consideration the increase in the weight of the body with age, it is evident that the respiratory activity is much greater in youth than in adult life. Andral and Gavarret do not give the weight of the subjects of their observations, but, as the weight generally does not diminish after maturity, there can be no doubt that there is a rapid diminution in the relative quantity of carbonic acid produced in old age.

Scharling, in a series of observations on a boy nine years of age and weighing 48·5 pounds, an adult of twenty-eight, and one of thirty-five years, the latter weighing 163·6 pounds, showed that the respiratory activity in the child was nearly twice as great, in proportion to his weight, as the average in the adults. It is seen, from the observations of Andral and Gavarret, that the absolute increase in the exhalation of carbonic acid from childhood to adult life is very slight in comparison with the natural increase in the weight of the body; showing that, proportionately, the exhalation of carbonic acid is greater in early life.

Influence of Sex.—All observers have found a marked difference between the sexes, in favor of the male, in the proportion of carbonic acid exhaled. Andral and Gavarret noted an absolute difference of about forty-five cubic inches per hour but did not take into consideration the differences in the weight of the body. Scharling, taking the proportion exhaled to the weight of the body, noted a marked difference in favor of the male.

The difference in the degree of muscular activity in the sexes is sufficient to account for the greater evolution of carbonic acid in the male, for this principle is exhaled in proportion to the muscular development of the individual; but there is an important difference connected with the variations with age, which depends upon the condition of the generative system of the female.

The absolute increase in the evolution of carbonic acid with age, in the female, is arrested at the time of puberty and remains stationary during the entire menstrual period, provided the menstrual flow occur with regularity. During this time, the average exhalation per hour is 714 cubic inches. After the cessation of the menses, the quantity gradually increases, until, at the age of sixty, it amounts to 915 cubic inches per hour. From the age of sixty to eighty-two, the quantity diminishes to 793, and finally to 670 cubic inches.

When the menses are suppressed, there is an increase in the exhalation of carbonic acid, which continues until the flow becomes reëstablished. In a case of pregnancy observed by Scharling, the exhalation was increased to about 885 cubic inches.

Influence of Digestion.—Almost all observers agree that the exhalation of carbonic acid is largely increased during digestion. Lavoisier and Séguin found that, in repose and fasting, the quantity exhaled per hour was 1,210 cubic inches, which was raised to 1,800 and 1,900 during digestion. Numerous experiments on animals have confirmed this statement. A very interesting series of observations on this point was made by Vierordt upon his own person. Taking his dinner at from 12·30 to 1 P. M., having noted the frequency of the pulse and respirations and the exhalation of carbonic acid at 12, he found, at 2 P. M., the pulse and respirations increased in frequency, the volume of expired air augmented, and that the carbonic acid exhaled had increased from 15·77 to 18·22 cubic inches per minute. In order to ascertain that this variation did not depend upon the time of day independently of the digestive process, he made a comparison at 12 M., at 1 and at 2 P. M. without taking food, which showed no notable variation, either in the pulse, number of respirations, volume of expired air, or quantity of carbonic acid exhaled. There can be no doubt that the exhalation of carbonic acid is notably increased during the functional activity of the digestive system.

The effect of inanition is to gradually diminish the exhalation of carbonic acid. Bidder and Schmidt noted the daily production of carbonic acid in a cat which was subjected to eighteen days of inanition, at the end of which time it died. The quantity diminished gradually from day to day, until, just before death, it was reduced a little more than one-half. Dr. Smith noted, in his own person, the influence of a fast of twenty-seven hours. There was a marked diminution in the quantity of air respired, in the quantity of vapor exhaled, in the number of respirations, and in the rapidity of the pulse. The exhalation of carbonic acid was diminished one-fourth. An interesting point in this observation was the fact that the quantity was as small four and a half hours after eating as at the end of the twenty-seven hours. "An increase of carbonic acid in the absence of food, at or near the period when it is usually increased by food," was also noted in the experiment by Dr. Smith.

Influence of Diet.—Regnault and Reiset, in their experiments on animals, studied the effect of different kinds of diet upon the relations of the quantity of oxygen absorbed to the carbonic acid exhaled. About the only conclusive and extended series of investigations on the influence of diet upon the absolute quantity of carbonic acid exhaled are those of Dr. Smith. This observer made a large number of experiments on the influence of various kinds of food and extended his inquiries into the influence of certain beverages, such as tea, coffee, cocoa, malt and fermented liquors. We have already fully described the method employed in these experiments, and the conclusions, which are of great interest and importance, are very exact and reliable.

Dr. Smith divides food into two classes, one which increases the exhalation of carbonic acid, which he calls respiratory excitants, and the other, which diminishes the exhalation, he calls non-exciters.

The following are the results of a large number of carefully-conducted observations upon four persons:

"The excito-respiratory are nitrogeneous food, milk and its components, sugars, rum, beer, stout, the cereals, and potato.

"The non-exciters are starch, fat, certain alcoholic compounds, the volatile elements of wines and spirits, and coffee-leaves.

"Respiratory excitants have a temporary action; but the action of most of them commences very quickly, and attains its maximum within one hour.

"The most powerful respiratory excitants are tea and sugar; then coffee, rum, milk, cocoa, ales, and chiccory; then casein and gluten, and lastly, gelatin and albumen. The amount of action was not in uniform proportion to their quantity. Compound aliments, as the cereals, containing several of these substances, have an action greater than that of any of their elements.

"Most respiratory excitants, as tea, coffee, gluten, and casein, cause an increase in the evolution of carbon greater than the quantity which they supply, while others, as sugar, supply more than they evolve in this excess, that is, above the basis. No substance containing a large amount of carbon evolves more than a small portion of that carbon in the temporary action occurring above the basis-line, and hence a large portion remains unaccounted for by these experiments."

The comparative observations of Dr. Smith upon the four persons who were the subjects of experiment demonstrated one very important fact; namely, that the action of different kinds of food upon respiration is modified by idiosyncrasies and the tastes of different individuals. For example, in experiments on his own person, certain articles which were agreeable to him excited the exhalation of carbonic acid; but in experimenting with the same articles upon Mr. Moul, to whom they were distasteful, he found the respiratory action diminished.

Quite a number of observers have noted the influence of alcohol upon the products of respiration; but the results of experiments have not been entirely uniform. Prout observed a constant diminution in the quantity of carbonic acid exhaled, under the influence of alcohol. This has been confirmed by the observations of Horn, Vierordt, and many others; but Hervier and Saint-Lager assert that the use of alcohol increases the exhalation of carbonic acid. In the experiments of Prout, a small quantity of wine taken fasting caused the proportion of carbonic acid in the expired air to fall immediately from 4 to 3 parts per 100. During the four hours following, it oscillated between 3·40, 3·10, and 3. The administration of a second dose, followed by some symptoms of intoxication, diminished the proportion to 2·70 per 100. Dr. Fyfe, of Edinburgh, showed that the depressing effects of an alcoholic excess were continued into the following day. Dr. Fyfe also noted a fact, important in this connection, namely, that the prolonged use of nitric acid and the condition of the system induced by the administration of mercurials were attended with a considerable diminution in the daily amount of carbonic acid exhaled by the lungs. In addition, Prout demonstrated that the exhalation of carbonic acid was diminished by the use of a concentrated infusion of tea, and Horn noted the same effect attending slight narcotism produced by smoking tobacco.

The observations of Dr. Smith, which were all made fasting, show a certain variation in the effects of different alcoholic beverages. His results are briefly the following:

"Brandy, whiskey, and gin, and particularly the latter, almost always lessened the respiratory changes recorded, while rum as commonly increased them. Rum-and-milk had a very pronounced and persistent action, and there was no effect on the sensorium. Ale and porter always increased them, while sherry wine lessened the quantity of air inspired, but slightly increased the carbonic acid evolved.

"The volatile elements of alcohol, gin, rum, sherry, and port-wine, when inhaled, lessened the quantity of carbonic acid exhaled, and usually lessened the quantity of air inhaled. The effect of fine old port-wine was very decided and uniform; and it is known that wines and spirits improve in aroma and become weaker in alcohol by age. The excito-respiratory action of rum is probably not due to its volatile elements."

From these facts, it would seem that the most constant effect of alcohol and of alcoholic liquors, such as wines and spirits, is to diminish the exhalation of carbonic acid. This effect is almost instantaneous, when the articles are taken into the stomach fasting; and when taken with the meals, the increase in carbonic acid which habitually accompanies the process of digestion is materially lessened. Rum, which Dr. Smith found to be a respiratory excitant, is an exception to this rule. Malt liquors seem to increase the exhalation of carbonic acid. With regard to alcohol itself, Dr. Smith says: "The action of pure alcohol was much more to increase than to lessen the respiratory changes, and sometimes the former effect was well pronounced."

Regarding as one of the great sources of carbonic acid the development of this principle in the tissues, whence it is taken up by the blood, Dr. Smith attributes the grateful and soothing influence of tea, coffee, *eau sucrée*, and the other beverages which he classes as respiratory excitants, to their action in facilitating the removal of this principle from the system. The presence of carbonic acid in the tissues and in the blood produces a sense of *malaise*, or depression, which we should suppose would be relieved by any thing which facilitates its elimination. It is undoubtedly this indefinite sense of discomfort which induces the act of sighing, by which the air in the lungs is more effectually renovated. This view is sustained by the fact that intellectual fatigue and mental emotions diminish the exhalation of carbonic acid. Apjohn cites an instance in which the proportion of carbonic acid in the expirations was reduced to 2·9 parts per 100 under the influence of mental depression.

We have already alluded to the modification in the exhalation of carbonic acid produced by tobacco.

Influence of Sleep.—All who have directed attention to the influence of sleep upon the respiratory products have noted a marked diminution in the exhalation of carbonic acid; but we again recur to the experiments of Dr. Smith for exact information on this point. Dr. Smith estimated the quantity of carbonic acid exhaled during six hours of sleep, at night, at 4,126 cubic inches. According to this observer, the quantity during the night is to the quantity during the day, in complete repose, as ten is to eighteen. During a light sleep, the exhalation was 10·32, and during profound sleep, 9·52 cubic inches per minute.

We have alluded to the great diminution in the quantity of oxygen consumed in hibernating animals while in a torpid condition. Regnault and Reiset found that a marmot in hibernation consumed only $\frac{1}{30}$ of the oxygen which he used in his active condition. In the same animal they noted an exhalation of carbonic acid equal to but little more than half the weight of oxygen absorbed; so that in this condition the diminution in the exhalation of carbonic acid is proportionately even greater than in the consumption of oxygen.

Influence of Muscular Activity.—Nearly all observers are agreed that there is a considerable increase in the exhalation of carbonic acid during and immediately following muscular exercise. In insects, Mr. Newport has found that a greater quantity is sometimes exhaled in an hour of violent agitation than in twenty-four hours of repose. In a drone, the exhalation in twenty-four hours was 0·30 of a cubic inch, and during violent muscular exertion the exhalation in one hour was 0·34. Lavoisier recognized the great influence of muscular activity upon the respiratory changes. In treating of the consumption of oxygen, we have quoted his observations on the relative quantities of air vitiated in repose and activity.

Vierordt, in a number of observations on the human subject, ascertained that moderate exercise increased the average quantity of air respired per minute by nearly nineteen cubic inches, and that there was an increase of 1·197 cubic inch per minute in the absolute quantity of carbonic acid exhaled.

The following results of the experiments of Dr. Edward Smith on the influence of exercise are very definite and satisfactory:

In walking at the rate of two miles an hour, the exhalation of carbonic acid during one hour was equal to the quantity produced during 1⅛ hour of repose with food, and 2½ hours of repose without food.

Walking at the rate of three miles per hour, one hour was equal to 2¾ hours with, and 3⅓ hours without food.

One hour's labor at the tread-wheel, while actually working the wheel, was equal to 4⅓ hours of rest with food, and 6 hours without food.

The various observers we have cited have remarked that, when muscular exertion is carried so far as to produce great fatigue and exhaustion, the exhalation of carbonic acid is notably diminished.

Influence of Moisture and Temperature.—Lehmann has shown that the exhalation of carbonic acid is much greater in a moist than in a dry atmosphere. This conclusion was the result of a number of experiments on birds and animals confined in air at different temperatures and different degrees of moisture. He found that 35¼ oz. av. weight of rabbits, at a temperature of about 100° Fahr., exhaled during an hour before noon, in a dry air, about 15 cubic inches of carbonic acid; while, in a moist air at the same temperature, the exhalation was about 22 cubic inches.

Disregarding observations on the influence of temperature in cold-blooded animals as inapplicable to the human subject, it has been ascertained that the exhalation of carbonic acid is much greater at low than at high temperatures, within the limits of heat and cold that are easily borne by the human subject; thus following the rule which governs the consumption of oxygen.

The experiments of Vierordt on the human subject show that there is an increase in the exhalation of carbonic acid of about one-sixth, under the influence of a moderate diminution in temperature. In these observations, the low temperatures ranged between 37·5° and 59°, and the high temperatures between 60·5° and 75·5° Fahr. He found the quantity of air taken into the lungs slightly increased at low temperatures. The absolute quantity of carbonic acid exhaled per minute was 18·27 cubic inches for the low temperatures, and 15·73 cubic inches for the high temperatures.

Influence of the Season of the Year.—It has been pretty well established by the researches of Dr. Smith, that spring is the season of the greatest, and fall the season of the least activity of the respiratory function.

The months of maximum are: January, February, March, and April.

The months of minimum are: July, August, and a part of September.

The months of decrease are: June and July.

The months of increase are: October, November, and December.

W. F. Edwards, in 1819, showed in a marked manner the influence of the seasons upon the respiratory phenomena in birds. In a series of very curious observations, which he repeatedly verified, it was demonstrated that the increase in the activity of respiration during the winter was to a certain extent independent of the immediate influence of the surrounding temperature. In the month of January, he confined six yellow-hammers in a receiver containing 71·4 cubic inches of air, carrying the temperature from 69° to 70° Fahr. The mean duration of their life was 62 minutes 25 seconds. In the months of August and September, he repeated the experiment on thirteen birds of the same species, at the same temperature. The mean duration of life was 82 minutes. These experiments have an important bearing on our views concerning the essential nature of the respiratory function. They seem to indicate that the respiratory processes are intimately connected with nutrition. Like the other nutritive phenomena, they undoubtedly vary at different seasons of the year and are to a certain extent independent of sudden and transitory conditions. During the winter, more air is habitually used than in summer, and the respiratory processes cannot be immediately brought down to the summer standard by a mere elevation of temperature.

Observations on the influence of barometric pressure are not sufficiently definite in their results to warrant any exact conclusions.

Some physiologists have attempted to fix certain hours of the day when the exhalation of carbonic acid is at its maximum or at its minimum; but the respiratory activity is influenced by such a variety of conditions, that it is impossible to do this with any degree of accuracy.

Relations between the Quantity of Oxygen consumed and the Quantity of Carbonic Acid exhaled.

Oxygen unites with carbon in certain proportions to form carbonic-acid gas, the volume of which is precisely equal to the volume of the oxygen which enters into its composition. In studying the relations of the volumes of these gases in respiration, we have a guide in the comparison of the volumes of the inspired and expired air. It is now generally recognized that the volume of air expired is less, at an equal temperature, than the volume of air inspired. Assuming, then, that the changes in the expired air, as regards nitrogen and all gases except oxygen or carbonic acid, are insignificant, it must be admitted that a certain quantity of the oxygen consumed by the economy is unaccounted for by the oxygen which enters into the composition of the carbonic acid exhaled. We have already noted that from $\frac{1}{70}$ to $\frac{1}{50}$, or about 1·4 to 2 per cent. of the inspired air is lost in the lungs; or it may be stated, in general terms, that the oxygen absorbed is equal to about five per cent. of the volume of air inspired, and the carbonic acid exhaled, only about four per cent. A certain amount of the deficiency in volume of the expired air is to be accounted for, then, by a deficiency in the exhalation of carbonic acid.

The experiments of Regnault and Reiset, to which frequent reference has been made, have a most important bearing on the question under consideration. As these observers were able to accurately measure the entire quantities of oxygen consumed and carbonic acid produced in a given time, the relation between the two gases was kept constantly in view. They found great variations in this relation, mainly dependent upon the regimen of the animal. The total loss of oxygen was found to be much greater in carnivorous than in herbivorous animals; and, in animals that could be subjected to a mixed diet, by regulating the food, this was made to vary between the two extremes. The mean of seven experiments on dogs showed that, for every 1,000 parts of oxygen consumed, 745 parts were exhaled in the form of carbonic acid. In six experiments on rabbits, the mean was 919 for every 1,000 parts of oxygen.

In animals fed on grains, the proportion of carbonic acid exhaled was greatest, sometimes passing a little beyond the volume of oxygen consumed.

"The relation is nearly constant for animals of the same species which are subjected to a perfectly uniform alimentation, as is easy to realize as regards dogs; but it varies notably in animals of the same species, and in the same animal, submitted to the same regimen, but in which we cannot regulate the alimentation, as in fowls."

When herbivorous animals were entirely deprived of food, the relation between the gases was the same as in carnivorous animals.

The final result of the experiments of Regnault and Reiset was, that the "relation between the oxygen contained in the carbonic acid and the total oxygen consumed, varies, in the same animal, from 0·62 to 1·04, according to the regimen to which it is subjected." These observations on animals have been confirmed in the human subject by M. Doyère, who found a great variation in the relations of the two gases in respiration; the volume of carbonic acid exhaled varying between 1·087 and 0·862 for 1 part of oxygen consumed.

The destination of the oxygen which is not represented in the carbonic acid exhaled is obscure. Some have thought that it unites with hydrogen to form water; but there is no satisfactory evidence of the formation of water in the economy, and researches have failed to show that there is more thrown off from the body than is taken in with food and drink.

The variations in the relative volumes of oxygen consumed and carbonic acid produced in respiration are not favorable to the hypothesis that the carbonic acid is the result of a direct action of oxygen upon carbonaceous matters. We should hardly expect a definite relation to exist between these two gases in respiration, when we find carbonic acid exhaled in the absence of oxygen.

Many of the points which we have considered with relation to the variations in the exhalation of carbonic acid have been investigated by experiments in Pettenkofer's chamber, and the results very nearly correspond with the observations of Scharling, Smith, and others which we have quoted.

Sources of Carbonic Acid in the Expired Air.—All the carbonic acid in the expired air comes from the venous blood, where it exists in two forms; in a free state in simple solution, or at least in a state of very feeble combination, and in union with bases, forming the carbonates and bicarbonates. That which exists in solution in the blood is simply exhaled. The alkaline carbonates and bicarbonates of the blood, coming to the lungs, meet with pneumic acid (discovered by Verdeil in 1851), and are decomposed, giving rise to a farther evolution of gas. It is pneumic acid which gives the constant acid reaction to the tissue of the lungs. This principle is found in the pulmonary parenchyma at all periods of life, from which it may be extracted by the proper manipulations and obtained in a crystalline form. Its quantity is not very great. The lungs of a female who suffered death by decapitation contained about 0·77 of a grain.

The action of pneumic acid upon the bicarbonates in the blood has been illustrated in a marked manner by Bernard. When bicarbonate of soda is injected into the jugular of a living animal, a rabbit, for example, it is decomposed as fast as it gets to the lungs, and carbonic acid is evolved. This experiment produces no inconvenience to the animal when the bicarbonate is introduced slowly; but, when it is injected in large quantity, the evolution of gas in the lungs is so great as to fill the pulmonary structure and even the heart and great vessels, and death is the result.

Exhalation of Watery Vapor.—The fact that the expired air contains a considerable quantity of watery vapor has long been recognized; and most of the earlier experimenters who directed their attention to the phenomena of respiration made the estimation of the quantity exhaled, and the laws which regulate pulmonary transpiration, the subject of investigation. It is evident that there must be many circumstances materially influencing this process, such as the hygrometric condition of the atmosphere, temperature, extent of respiratory surface, etc., which are of sufficient importance to demand special consideration. In many points of view, also, it is interesting to know the absolute quantity of aqueous exhalation from the lungs.

When the surrounding atmosphere has a temperature below 40° or 43° Fahr., a distinct cloud is produced by the condensation of the vapor of the breath. By breathing upon any polished surface, it is momentarily tarnished by the condensed moisture. Although the fact that watery vapor is contained in the breath is thus easily demonstrated, the estimation of its absolute quantity presents difficulties which were not overcome by the older physiologists. With the present improved methods of analysis, however, there are many very accurate means of estimating watery vapor. One method is by the use of Liebig's bulbs filled with sulphuric acid, or tubes filled with chloride of calcium, both of which substances have a great avidity for water. From a large number of observations on his own person and eight others, collecting the water by sulphuric acid, Valentin made the following estimate of the weight of water exhaled from the lungs in twenty-four hours:

In his own person, the exhalation in twenty-four hours was 6,055 grains.

In a young man of small size, the quantity was 5,042 grains.

In a student rather above the ordinary height, the quantity was 11,930 grains.

The mean of his observations gave a daily exhalation of 8,333 grains, or about $1\frac{1}{5}$ lb. av.

The extent of respiratory surface has a very marked influence on the quantity of watery vapor exhaled. This fact is very well shown by a comparison of the exhalation in the adult and in old age, when the extent of respiratory surface is much diminished. Barral found the exhalation in an old man less than half that of the adult. It is evident that the absolute quantity of vapor exhaled is increased when respiration is accelerated. The quantity of water in the blood also exerts an important influence. Valentin found that the pulmonary transpiration was more than doubled in a man immediately after drinking a large quantity of water.

The vapor in the expired air is derived from the entire surface which is traversed in respiration, and not exclusively from the air-cells. The air which passes into the lungs derives a certain amount of moisture from the mouth, nares, and trachea. The great vascularity of the mucous membranes in these situations as well as of the air-cells, and the great number of mucous glands which they contain, serve to keep the respiratory surfaces constantly moist. This is important, for only moist membranes allow the free passage of gases, which is of course essential to the process of respiration.

Exhalation of Ammonia, Organic Matter, etc.—Ammonia has long been recognized as an exhalation from the human body in health, from the skin as well as the lungs. Dr. Richardson calls attention, in his essay on the "Coagulation of the Blood," to the observations of Mr. Reade, Dr. Reuling, Viale and Latini, and others, on this point. Reuling has shown that the quantity of ammonia in the expired air is increased in certain diseases, particularly in uræmia. Its characters in the expired air are frequently so marked, that patients who are entirely unacquainted with the pathology of uræmia sometimes recognize an ammoniacal odor in their own breath.

The pulmonary surface exhales a small quantity of organic matter. This has never been collected in sufficient quantity to enable us to recognize in it any peculiar or distinctive properties, but its presence may be demonstrated by the fact that a sponge completely saturated with the exhalations from the lungs, or the vapor from the lungs condensed in a glass vessel, will undergo putrefaction, which is a property distinctive of organic substances.

It is well known that certain substances which are only occasionally found in the blood may be eliminated by the lungs. Certain odorous principles in the breath are pretty constant in those who take liquors habitually in considerable quantity. The odor of garlics, onions, turpentine, and many other principles which are taken into the stomach, may be recognized in the expired air.

The action of the lungs in the elimination of certain gases, which are poisonous in very small quantities when they are absorbed in the lungs and carried to the general system in the arterial blood, is very well shown by the experiments of Bernard. Sulphuretted hydrogen, which produces death in a bird when it exists in the atmosphere in the proportion of one to eight hundred, may be taken in solution into the stomach with impunity and even be injected into the venous system; in both instances being eliminated by the lungs with great promptness and rapidity. The lungs, while they present an immense and rapidly absorbing surface for volatile poisonous substances, are capable of relieving the system of some of these substances by exhalation when they find their way into the veins.

Exhalation of Nitrogen.—The most accurate direct experiments, particularly those of Regnault and Reiset, show that the exhalation of a small quantity of nitrogen is a pretty constant respiratory phenomenon. From a large number of experiments on dogs, rabbits, fowls, and birds, these observers came to the conclusion that, when animals are subjected to their habitual regimen, they exhale a quantity of nitrogen equal in weight to from $\frac{1}{100}$ to $\frac{1}{50}$ of the weight of oxygen consumed. In birds, during inanition, they sometimes observed an absorption of nitrogen, but this was rarely seen in mammals. Boussingault, estimating the nitrogen taken into the body and comparing it with the entire quantity discharged, arrived at the same results in experiments upon a cow. Barral, by the same method, confirmed these observations by experiments on the human subject. Notwithstanding the conflicting testimony of the older physiologists, there can now be no doubt that, under ordinary physiological conditions, there is an exhalation by the lungs of a small quantity of nitrogen.

Changes of the Blood in Respiration (Hœmatosis).

It is to be expected that the blood, receiving, on the one hand, all the products of digestion, and, on the other, the products of disassimilation or decay of the tissues, connected with the lymphatic system, and exposed to the action of the air in the lungs, should present important differences in composition in different parts of the vascular system.

In the first place, there is a marked difference in color, composition, and properties, between the blood in the arteries and in the veins; the change from venous to arterial blood being effected almost instantaneously in its passage through the lungs. The blood which goes to the lungs is a mixture of the fluid collected from all parts of the body; and we have seen that it presents great differences in its composition in different parts of the venous system. In some veins it is almost black, and in some, nearly as red as in the arteries. In the hepatic vein it contains sugar, and its nitrogenized constituents and corpuscles are diminished; in the portal vein, during digestion, it contains materials absorbed from the alimentary canal; and, finally, there is every reason to suppose that parts which require different materials for their nutrition and produce different excrementitious principles exert different influences on the constitution of the blood which passes through them. After this mixture of different kinds of blood has been collected in the right side of the heart and passed through the lungs, it is returned to the left side and sent to the system, thoroughly changed and renovated, and, as arterial blood, it has a nearly uniform composition, as far as can be ascertained, in all parts of the system. The change, therefore, which the blood undergoes in its passage through the lungs, is the transformation of the mixture of venous blood from all parts of the organism into a fluid of uniform character, which is capable of nourishing and sustaining the function of every tissue and organ of the body.

The capital phenomena of respiration, as regards the air in the lungs, are loss of oxygen and gain of carbonic acid, the other phenomena being accessory and comparatively unimportant. As the blood is capable of holding gases in solution, in studying the essential changes which this fluid undergoes in respiration, we look for them in connection with the proportions of oxygen and carbonic acid before and after it has passed through the lungs. In respiration, the most marked effect on the venous blood is change in color.

Difference in Color between Arterial and Venous Blood.—We have already considered this in treating of the properties of the blood, and shall take up in this connection only the cause of the remarkable change in the color of the blood in the lungs. This change is instantaneous, and, long before the discovery of oxygen by Priestley, was recognized by Lower, Goodwyn, and others, as due to the action of the air.

The influence of air in changing the color of venous blood may be noted in blood which has been drawn from the body, as is exemplified by the red color of that portion of a clot, or the surface of defibrinated venous blood, which is exposed to the air. If we cut into a clot of venous blood, the interior is almost black, but it becomes red on exposure to the air for a very few seconds.

We have been in the habit of illustrating the physiological influence of the air on venous blood by the following simple experiment: Removing the lungs of an animal (a dog) just killed, the nozzle of a syringe is secured in the pulmonary artery by a ligature, and a canula, connected with a rubber tube which empties into a glass vessel, is secured in the pulmonary vein. Adapting a bellows to the trachea, we imitate the process of respiration; and, if defibrinated venous blood be carefully injected through the lungs, it will be returned by the pulmonary vein, presenting the bright-red color of arterial blood. When the artificial respiration is interrupted, the blood passes through the lungs without change.[1] In exposing the thoracic organs and keeping up artificial respiration, repeating the celebrated experiment of Robert Hook, made before the Royal Society, in 1664, we can see, through the thin walls of the auricles, the red color of the blood on the left side contrasting with the dark venous blood on the right.

Since the discovery of oxygen, it has been ascertained that this is the only constituent of the air which is capable of arterializing the blood. Priestley showed that venous blood is not changed in color by nitrogen, hydrogen, or carbonic acid; while all these gases, by displacing oxygen, will change the arterial blood from red to black.[2]

The elements of the blood which absorb the greater part of the oxygen are the red corpuscles. While the plasma will absorb, perhaps, twice as much gas as pure water, it has been shown by Magnus and by Gay-Lussac that the corpuscles will absorb from ten to thirteen times as much. By some the proportion is put much higher. According to the late researches of Fernet, which have been confirmed by Lothar Meyer, the volume of oxygen fixed by the corpuscles is about twenty-five times that which is dissolved in the plasma.

Comparison of the Gases in Venous and Arterial Blood.—The demonstration of the fact that free oxygen and carbonic acid exist in the blood, with a knowledge of the relative proportion of these gases in the blood before and after its passage through the lungs, is a point hardly second in importance to the relative composition of the air before and after respiration. The idea enunciated by Mayow, about two hundred years ago, that "there is something in the air, absolutely necessary to life, which is conveyed into the blood," except that the vivifying principle is not named or its other properties described, expresses what we now consider one of the great objects of respiration. This is even more strictly in accordance with facts than the idea of Lavoisier, who supposed that all the chemical processes of respiration took place in the lungs. Mayow also described the evolution of gas from blood placed in a vacuum. Many observers have since succeeded in extracting gases from the blood by various processes. Sir Humphry Davy induced the evolution of carbonic acid by raising arterial blood to the temperature of 200° Fahr., and venous blood to a temperature of 112°; Stevens and others disengaged gas by displacement with hydrogen, nitrogen, or the ordinary atmosphere; but, notwithstanding this, before the experiments of Magnus, in 1837, many denied the existence in the blood of any free gas whatsoever.

Analysis of the Blood for Gases.—There were certain grave sources of error in the method employed by Magnus, which render his observations of little value, except as demonstrating that oxygen, carbonic acid, and nitrogen may be extracted by the air-pump from both arterial and venous blood. The only source of error in the results which he fully recognized lay in the difficulty in extracting the entire quantity of gas in solution; but a careful study of his essay shows another element of inaccuracy which is even more important. The relative quantities of oxygen and carbonic acid in any single

[1] This demonstration is very striking, especially if we use a syringe with a double nozzle, one point secured in the pulmonary artery, and the other simply carrying the blood by a rubber tube into a glass vessel. Receiving the blood which passes through the lungs and that which simply passes through the tube, into two tall glass vessels, the one is of a bright red, and the other retains its dark color. In preparing for the experiment it is necessary, immediately after removing the lungs from the animal, to inject them with a little defibrinated blood, so as to remove the coagulating blood from the pulmonary capillaries, which would otherwise become obstructed. The injection should be made gently and gradually, to avoid extravasation. Defibrinated ox-blood may be used. The most convenient way to secure the canulæ in the vessels is to push them into the pulmonary artery through the right ventricle, and into the pulmonary vein through the left auricle.

[2] Carbonic oxide and nitrous oxide have a strong affinity for the blood-corpuscles and become fixed in them, the former giving the blood a vivid red color. Sugar and many salts will also redden venous blood. These agents, however, do not impart the physiological properties of arterial blood.

specimen of blood present great variations, dependent upon the length of time that the blood has been allowed to stand before the estimate of the gases is made. As it is impossible to make this estimate immediately after the blood is drawn, on account of the froth produced by agitation with a gas when the method by displacement is employed, and the bubbling of the gas when extracted by the air-pump, this objection is fatal. It is necessary to wait until the froth has subsided before attempting to make an accurate estimate of the volume of gas given off. The following observation of Magnus illustrates this fact. The observation was on the human blood, six hours after it had been thoroughly mixed with hydrogen:

Blood of Man.	*Carbonic Acid.*
4·077 cubic inches.	·013 cubic inches.
3·650 "	0·781 "
3·838 "	1·355 "

After twenty-four hours, at the end of which time the blood had no odor:

4·077 cubic inches.	1·517 cubic inches.
3·650 "	1·456 "
3·833 "	2·075 "

The excess of carbonic acid found twenty-four hours after over the quantity found six hours after, in the first and third specimens, is a little more than fifty per cent., while in the second specimen it is very nearly one hundred per cent. In these analyses, the proportion of oxygen is not given. The question naturally arises as to the source of the carbonic acid which was evolved during the last eighteen hours of the observation. This is evident, when we consider one of the important properties of the blood. A number of years ago, Spallanzani demonstrated that, in common with other parts of the body, fresh blood removed from the body has, of itself, the property of consuming oxygen; and W. F. Edwards has shown that the blood will exhale carbonic acid. In 1856, Harley, by a series of ingenious experiments, found that blood, kept in contact with air in a closed vessel for twenty-four hours, consumed oxygen and gave off carbonic acid. More recently, Bernard has shown that, for a certain time after the blood is drawn from the vessels, it will continue to consume oxygen and exhale carbonic acid. If all the carbonic acid be removed from a specimen of blood by treating it with hydrogen, and if it be allowed to stand for twenty-four hours, another portion of gas can be removed by again treating it with hydrogen, and still another quantity by treating it with hydrogen a third time. From these facts it is clear that, in the experiment of Magnus, the excess of carbonic acid involved a post-mortem consumption of oxygen; and no analyses made in the ordinary way, by displacement with hydrogen or by the air-pump, in which the blood must necessarily be allowed to remain in contact with oxygen for a number of hours, can be accurate. The only process which can give us a rigorous estimate of the relative quantities of oxygen and carbonic acid in the blood is one in which the gases can be estimated without allowing the blood to stand, or in which the formation of carbonic acid in the specimen, at the expense of the oxygen, is prevented. All others will give a less quantity of oxygen and a greater quantity of carbonic acid than exists in the blood circulating in the vessels or immediately after it is drawn from the body.

A solution of this important and difficult problem in the analysis of the blood has been attained by Bernard. This observer made a great number of experiments in the hope of discovering some means by which the post-mortem consumption of oxygen by the blood-corpuscles could be arrested. He found, finally, that carbonic oxide, one of the most active of the poisonous gases, had a remarkable affinity for the blood-corpuscles. When taken into the lungs, it is absorbed by and becomes fixed in the corpuscles, effectually preventing the consumption of oxygen and the production of carbonic acid, which normally takes place in the capillary system and which is one of the indispensable conditions of nutrition. The mechanism of poisoning by the inhalation of this gas is by its fixation in the blood-corpuscles, their consequent paralysis, and the arrest of their function as respiratory organs. As it is the continuance of this transformation of oxygen into carbonic acid, after the blood is drawn from the vessels, which interferes with the ordinary analysis of the blood for gases, we might expect to extract all the oxygen if we could immediately saturate the blood with carbonic oxide. The preliminary experiments of Bernard on this point are conclusive. He ascertained that, by mixing carbonic oxide in sufficient quantity with a specimen of fresh arterial blood, in about two hours, all the oxygen which it contained was displaced. Introducing a second quantity of carbonic oxide after two hours, and leaving it in contact with the blood for an hour, a quantity of oxygen was removed so small that it might almost be disregarded. A third experiment on the same blood failed to disengage any oxygen or carbonic acid.

The view entertained by Bernard of the action of carbonic oxide in displacing the oxygen of the blood is, that the former gas has a remarkable affinity for the blood-corpuscles, in which nearly all the oxygen is contained, and when brought in contact with them unites with the organic matter, setting free the oxygen, in the same way that the acid entering into the composition of a salt is set free by any other acid which has a stronger affinity for the base. There is every reason to suppose that this view is correct, as carbonic oxide is much less soluble than oxygen and as it has the property of disengaging this gas only from the blood, leaving the other gases still in solution.

As carbonic oxide displaces the oxygen alone, it is necessary to resort to some other process, in addition to this, to disengage the other gases contained in the blood. It is only necessary to arrest the action of the corpuscles upon the oxygen, and then the gases may be set free by the air-pump or any method which may be convenient. The method adopted by Lothar Meyer, Bernard, Ludwig, and Gréhant for the disengagement of all the gases contained in the blood is first to displace the oxygen by carbonic oxide, using about two-thirds of gas by volume to one-third of blood, then to attach the tube to a column of mercury and subject the blood to the barometric vacuum, which sets free the carbonic acid and the nitrogen. The results obtained by this method correspond with our ideas concerning the nature of the respiratory process; and analyses of the blood taken at different periods show variations in the quantities of oxygen in the arterial, and carbonic acid in the venous blood, corresponding with some of the variations which we have noted in the loss of oxygen and gain of carbonic acid in the air in respiration.

In drawing the blood for analysis, Bernard takes the fluid directly from the vessels by a syringe and passes it under mercury into a tube, in such a way that it does not come in contact with the air. In this tube, which is graduated, the blood is brought in contact with carbonic oxide, which displaces the oxygen from the corpuscles and prevents the formation of carbonic acid at the expense of a portion of the oxygen. The tube is then connected with an apparatus by which the atmospheric pressure is removed. In this way, nearly all the gases contained in the blood are disengaged; but, according to most observers, a small quantity of carbonic acid remains in the blood in combination. This may be removed by the introduction into the apparatus of a small quantity of tartaric acid. It is justly remarked by Bert, in his admirable work on respiration, that, as the apparatus for the exhaustion of air has been made more and more nearly perfect, the quantity of carbonic acid in combination has seemed less and less. By far the greatest quantity of the excrementitious carbonic acid in the blood is extracted by the removal of atmospheric pressure in the most carefully-perfected apparatus.

The analyses of Bernard, who obtained from fifteen to twenty per cent. of oxygen in volume from the arterial blood, show the great imperfection of the process employed by Magnus, who obtained from the arterial blood of horses and calves a mean of but 2·44 per cent. of oxygen. It does not seem necessary, therefore, to discuss the criticisms of the results obtained by Magnus which were made by Gay-Lussac and Magendie, soon after their publication, and more recently by Harley and others.[1]

Bernard's experiments were made chiefly on dogs and had special reference to the proportion of oxygen in the blood. In two specimens taken from a dog in good condition, a specimen of arterial blood, drawn from the vessels by a syringe and put in contact with carbonic oxide without being exposed to the air, was found to contain 18·28 per cent., and a specimen of venous blood, taken in the same way, 8·42 per cent., in volume, of oxygen. The proportion of gases in the blood is found to vary very considerably under different conditions of the system, particularly with reference to the digestive process. The following are the general results of later observations, showing the differences and variations in the proportions of all the gases in arterial and venous blood.

Arterial blood, while an animal is fasting, contains from nine to eleven parts per hundred of oxygen. In full digestion, the proportion is raised to seventeen, eighteen, or even twenty parts per hundred. The proportion varies in different animals, being much greater, for example, in birds than in mammals.

The quantity of carbonic acid is even more variable than the quantity of oxygen. During digestion there are from five to six parts per hundred of free carbonic acid in the arterial blood. During the intervals of digestion this quantity is reduced to almost nothing; and, after fasting for twenty-four hours, frequently not a trace is to be discovered.[2]

Venous blood always contains a large quantity of carbonic acid, both free in solution and combined with bases. This quantity varies in different parts of the venous system and bears a relation to the color of the blood. It is well known that the venous blood coming from some glands is dark during the intervals of secretion and nearly as red as arterial blood during their functional activity. In the venous blood from the submaxillary gland of a dog, Bernard found 18·07 per cent. of carbonic acid during repose and 10·14 per cent. during secretion. The blood coming from the muscles is the darkest in the body and contains the greatest quantity of free carbonic acid. The quantity of free carbonic acid is immensely increased in the venous blood during digestion. It is owing to this fact that the gas then exists in quantity in the arterial blood. Bearing in mind the fact that the proportion of gases in the arterial and venous blood varies considerably under different conditions of the system and that it is especially variable in the blood of different veins, we may take the following, which we quote from Bert, as the average results obtained by the most recent German observers:

	O.	CO_2 disengaged by a vacuum.	CO_2 in combination.	CO_2 total.	N.	Total gas in volume per 100.
"Arterial blood ..	15·03	27·99	1·15	29·14	1·60	45·77
Venous blood...	8·17	31·27	2·38	33·65	1·37	43·19

"If we now examine the blood coming from different parts of the body, we find that the blood of the hepatic veins is poorer in oxygen and richer in carbonic acid than the general venous blood; that the blood of the portal vein presents the same characters to a higher degree; that the blood of the muscles in contraction presents the same relations as compared with the blood of muscles in repose or paralyzed; that, on the other hand, the blood of the glands has more oxygen during their activity than during their repose.

[1] To Magnus belongs the credit of demonstrating the important fact that oxygen, carbonic acid. and nitrogen can be extracted from the blood by removing the atmospheric pressure. Before his observations, Gmelin, Mitscherlich, and Tiedemann placed venous blood in a tube over mercury in the receiver of an air-pump, and, by removing the pressure as far as possible, caused the mercury to descend. On admitting air into the receiver and restoring the pressure, the mercury ascended, with the blood, again filling the tube completely. From this they reasoned that there was no free carbonic acid in the blood. By passing up a little acetic acid, carbonic acid was set free, which led them to believe that all the carbonic acid was in combination. Magnus showed that the reason why other observers had failed to extract gas by means of the air-pump was that the rarefaction of the air was not carried sufficiently far.

[2] These results are quoted from Bernard and were given in his lectures delivered at the College of France in the summer of 1861. More recent observations by German physiologists have shown that Bernard's estimates of the proportions of carbonic acid were much too low.

"If we compare the venous blood of the right side of the heart with the arterial blood of the left side, we find that the latter is richer in oxygen and poorer in carbonic acid. In examining this more closely, we see that the difference in the oxygen is greater than in the carbonic acid; this being in accordance with the well-known fact that animals absorb more oxygen than is equivalent to the carbonic acid exhaled."

These facts coincide with the views which are now held regarding the essential processes of respiration. The blood going to the lungs contains carbonic acid and but a small proportion of oxygen. In the lungs, carbonic acid is given off, appearing in the expired air, and the oxygen which disappears from the air is carried away by the arterial blood.

Nitrogen of the Blood.—As far as is known, nitrogen has no very important office in the process of respiration. There is sometimes a slight exhalation of this gas by the lungs, and analyses have demonstrated its existence in solution in the blood. Magnus found generally a larger proportion in the arterial than in venous blood, although, in one instance, there was a larger proportion in the venous blood. It is not absolutely certain whether the nitrogen which exists in the blood be derived from the air or from the tissues. Its almost constant exhalation in the expired air would lead to the supposition that it is produced in small quantity in the system or supplied by the food. There is no evidence that nitrogen enters into combination with the blood-corpuscles; it exists simply in solution in the blood, which is capable of absorbing about ten times as much as pure water. Nothing is known with regard to the relations of the free nitrogen of the blood to the processes of nutrition.

Condition of the Gases in the Blood.—It is now pretty generally admitted that the oxygen of the blood exists, not in simple solution, but in a condition of feeble combination with certain of the constituents of the blood-corpuscles, particularly the coloring matter. In studying the composition of the corpuscles, we have seen that, when air is admitted to venous blood, oxygen unites with the hæmaglobine, forming oxyhæmaglobine. Carbonic oxide, which has a great affinity for the corpuscles, displaces almost immediately all the oxygen which the blood contains. When the corpuscles are destroyed, as they may be readily by receiving fresh blood into a quantity of pure water, the red color is instantly changed to black.

Carbonic acid is more easily exhaled from the blood than oxygen. It was this principle which was obtained by those who first succeeded in extracting gas from the blood. While there is every reason to suppose that oxygen is in combination with the blood-corpuscles, carbonic acid seems to be in a condition of simple solution and is contained more especially in the plasma. What may be considered as the free carbonic acid of the blood behaves in all regards like a gas simply held in solution. The view that it is held in solution chiefly in the plasma is sustained by the fact that serum will absorb more carbonic acid than an equal volume of defibrinated blood.

Liebig has shown that the phosphate of soda, one of the constituents of the blood, influences to a remarkable degree the quantity of carbonic acid which can be held in solution by any liquid. One hundredth of a part of this salt in pure water will double its capacity for dissolving carbonic acid. When blood is in contact with a certain quantity of air, oxygen is consumed and carbonic acid is exhaled. The fact that carbonic oxide, which has such a remarkable affinity for the corpuscles, displaces oxygen almost exclusively, is another argument in favor of the view that the carbonic acid is contained mainly in the plasma.

The carbonic acid which is formed in the tissues and is taken up by the blood in its passage through the capillaries exists in this fluid in two forms: one, in simple solution, chiefly in the plasma, and the other, in a state of such loose chemical combination in the bicarbonates that it may be disengaged by displacement by another gas and is readily set free by pneumic acid. This gas is a product of excretion and is not engaged in any of the vital functions; while oxygen, which has an all-important function to perform, unites immediately with the blood-corpuscles and is not easily disengaged except when it undergoes transformation in the process of nutrition. In addition to this excrementitious carbonic acid, there is another portion which is a permanent constituent of the blood, in the carbonates, and cannot be set free without the use of reagents.

Nitrogen exists in the blood in the same condition of solution in the plasma as carbonic acid.

Mechanism of the Interchange of Gases between the Blood and the Air in the Lungs.—The gases from the air pass into the blood, and the gases of the blood are exhaled through the delicate membrane which separates these two fluids, in accordance with laws which are now well understood. The first to point out the power of gases thus to penetrate and pass through membranes was the late Dr. J. K. Mitchell, of Philadelphia. His attention was first directed to this subject by noticing the escape of gas from gum-elastic balloons filled with hydrogen. Observations on the lungs of the snapping turtle filled with air and placed in an atmosphere of carbonic acid or nitrous oxide, showed a very rapid passage of gas from the exterior to the interior. Dr. Mitchell recognized the passage of gases through membranes into liquids and the exhalation of gases which were in solution in these liquids. He noted this action in the absorption of oxygen and the exhalation of carbonic acid in the lungs, although he fell into the error of supposing that there was no carbonic acid in solution in the blood and that it was exhaled as soon as formed. A few years later, Dr. Rogers, of Philadelphia, enclosed a fresh pig's bladder, filled with venous blood, in a bell-glass of oxygen. In two hours a quantity of oxygen had been consumed and a large quantity of carbonic acid had made its appearance.

We have already seen that the blood is exposed to the air in the lungs, separated from it only by a very delicate membrane, over an immense surface. The membrane, far from interfering with the interchange of gases, actually favors it; and thus, in obedience to the laws which regulate endosmosis between gases and liquids, the oxygen is continually passing into the blood and the free carbonic acid is exhaled.

General Differences in the Composition of Arterial and Venous Blood.—All observers agree that there are certain marked differences in the composition of arterial and venous blood, aside from their free gases. The arterial blood contains less water and is richer in organic and most inorganic constituents than the venous blood. It also contains a larger proportion of corpuscles. It is more coagulable and offers a larger and firmer clot than venous blood. The only principles which are constantly more abundant in venous blood are water and the alkaline carbonates. According to Longet, 10,000 parts of venous blood contained 12·3 parts of carbonic acid combined, and the same quantity of arterial blood contained but 8·3 parts. The deficiency of water in the blood which comes from the lungs is readily explained by the escape of watery vapor in the expired air.

An important distinction between arterial and venous blood is one to which we have already incidentally alluded; viz., that the former has a uniform composition in all parts of the arterial system, while the composition of the latter varies very much in the blood coming from different organs. Arterial blood is capable of carrying on the processes of nutrition, while venous blood is not and cannot even circulate freely in the systemic capillaries.

Relations of Respiration to Nutrition, etc.—It has been demonstrated that all tissues, so long as they retain their absolute integrity of composition, have the property of appropriating oxygen and exhaling carbonic acid, independently of the presence of blood; and that the arterial blood carries oxygen from the lungs to the tissues, there gives it up, and receives carbonic acid, which is carried by the venous blood to the lungs, to be exhaled.

From this fact alone, it is more than probable that respiration is inseparably connected with the general act of nutrition. Its processes must be studied, therefore, as they take place in the tissues and organs of the body. In the present state of the science, the questions which naturally arise in connection with the essential processes of respiration are the following:

1. In what way is oxygen consumed in the system?
2. How is carbonic acid produced by the system?
3. What is the nature of the processes which take place between the disappearance of oxygen and the evolution of carbonic acid?

When these questions are satisfactorily answered, we shall understand the essence of respiration; but, in reasoning on this subject, we must not fall into the error of assimilating the respiratory phenomena too closely to those with which we are acquainted as they occur in inorganic bodies. It must be remembered that in the organism we are dealing with principles which have the remarkable property of self-regeneration, and which, as a simple condition of normal existence, consume oxygen, when it is presented to them, and exhale carbonic acid. Without a proper supply of oxygen, the tissues die, lose these peculiar properties, and finally disappear by putrefactive decomposition. This consumption of oxygen cannot be regarded in any other light than as the appropriation, by a living part, of an element necessary to supply waste, in the same way as those materials which are ordinarily called nutritive are appropriated. That waste is continually going on there can be no doubt; and, as the production of urea, creatine, creatinine, cholesterine, etc., is, to a certain extent, independent of the absorption of food, so the production of carbonic acid is in a certain degree independent of the absorption of oxygen. How different are these phenomena from those which attend the combinations and decompositions of inorganic matters! As an example, let oxygen be brought in contact, under proper conditions, with iron. Under these circumstances, a union of iron and oxygen takes place, and a new substance, oxide of iron, is formed, which has peculiar and distinct properties. In the same way, carbonic acid may be disengaged from its combinations by the action of a stronger acid, which unites with the base and forms a new substance in no way resembling the original salt. To make the contrast still more striking, let fat be heated in oxygen or in the air until it undergoes combustion; it is then changed into carbonic acid and water, by a definite chemical reaction, and is utterly destroyed as fat.

In the living body the organic nitrogenized principles are in a condition of continual change, breaking down and forming various excrementitious principles, at the head of which may be placed carbonic acid. It is essential to life that these principles be maintained in their chemical integrity, which requires a supply of fresh matter as food, and, above all, a supply of oxygen. We put ourselves in the position of ignoring well-established facts and principles when we assimilate without reserve the process of the consumption of oxygen and production of carbonic acid by living organic bodies, to simple combustion of sugar or fat. The ancients saw that the breath was warmer than the surrounding air, that in the lungs the air took heat from the body, and, as they knew of no other changes in the air produced by respiration, they assumed that its object was simply to cool the blood. Lavoisier discovered that the air, containing oxygen, lost a portion of this principle in respiration and gained carbonic acid and watery vapor. He saw that this might be imitated by the combustion of hydro-carbons, such as exist in the blood. He called respiration a slow combustion and regarded as its principal office the maintenance of animal temperature. When it was shown by analyses of the blood for gases, that oxygen is not consumed in the lungs, but is taken up by the circulating fluid and carried all over the body, and that carbonic acid is brought from all parts by the blood to the lungs, these facts, taken in connection with the fact that the tissues have the property of consuming oxygen and exhaling carbonic acid, led physiologists to change the location of the combustive process from the lungs to the tissues.

We cannot stop at this point. Now it is known that the organic principles of the body, which form the basis of all tissues and organs, are continually undergoing change as a condition of existence; that they do not unite with any substance in definite chemical proportions, but that their particles, after a certain period of existence, degenerate into excrementitious substances and are regenerated by an appropriation and change of materials furnished by the blood. As far as the respiration of these parts is concerned, we can only say, that, in this process, carbonic acid is produced and oxygen is consumed. These facts show that respiration is essentially a phenomenon of nutrition, possessing a degree of complexity certainly equal to that of the other nutritive processes. It must be acknowledged that thus far its cause and intimate nature have eluded investigation. In respiration by the tissues, no one has yet been able to give the cause of the absorption of oxygen or the exhalation of carbonic acid, or to demonstrate the condition in which oxygen exists when once appropriated, or the particular changes which take place and the principles which are lost, in the formation of carbonic acid.

The views of physiologists with regard to the essential processes of respiration, before the time of Lavoisier, have barely an historical interest at the present day, except the remarkable idea of Mayow, which comprehended nearly the whole process and which was unnoticed for about a hundred years. It is not our object to dwell upon the various theories which have been advanced from time to time, or even to fully discuss, in this connection, the combustion-theory as proposed by Lavoisier and modified by Liebig and others. Although this theory is nominally received by many physiologists of the present day, it will be found that most of them, in accordance with the facts which have since been developed, really regard respiration as connected with nutrition. They only differ from those who reject the combustion-theory, in their definition of the term combustion. Lavoisier regarded respiration as a slow combustion of carbon and hydrogen; and, if every rapid or slow combination of oxygen with any other body be considered a combustion, this view is absolutely correct and was proven when it was shown that oxygen united with any of the tissues. Longet says that since the time of Lavoisier it is agreed to give the above signification to the word combustion; but this must simply be for the purpose of retaining the name applied by Lavoisier to the respiratory process, while its signification is altered to suit the facts which have since taken their place in science. There is no doubt that combustion is generally regarded as signifying the direct and active union of oxygen with certain principles which commonly contain carbon and hydrogen; and the immediate products of this union are carbonic acid, water, and, incidentally, heat and light. It is certain that oxygen does not unite in the body directly with carbon and hydrogen, although it is consumed and carbonic acid and water are produced in respiration. Important intermediate phenomena take place, and we do not therefore fully express the respiratory process by the term combustion. The researches of Spallanzani, W. F. Edwards, Collard de Martigny, and others, who have demonstrated the abundant exhalation of carbonic acid by animals and by tissues deprived of oxygen, show that it is not a product of combustion of any of the principles of the organism. Rejecting this hypothesis as insufficient to explain the intimate nature of the respiratory process, it remains to be seen how satisfactorily, in the present state of the science, it is possible to answer the several questions we have proposed.

1. In what way is the oxygen consumed in the system? Oxygen taken from the air is immediately absorbed by, and enters into the composition of the red corpuscles. Part of the oxygen disappears in the red corpuscles themselves, and carbonic acid is given off. To how great an extent this takes place it is impossible to say; but it is evident, even from a study of the methods of analysis of the blood for gases, that the property of absorbing oxygen and giving off carbonic acid, which Spallanzani demonstrated to belong to the tissues, is possessed as well by the red corpuscles. During life it is not possible to determine how far this takes place in the blood and how far in the tissues. The theory has been proposed that all the respiratory change takes place in the blood as

it circulates; but the avidity of the tissues for oxygen and the readiness with which they exhale carbonic acid leave no room for doubt that much of this change is effected in their substance.

Oxygen, carried by the blood to the tissues, is appropriated and consumed in their substance, together with the nutritive materials with which the circulating fluid is charged. We are acquainted with some of the laws which regulate its consumption but have not been able to follow it out and ascertain the exact nature of the changes which take place. All that we can say definitely on this point is, that it unites with the organic principles of the system, satisfying the "respiratory sense" and supplying an imperative want which is felt by all animals and which extends to all parts of the organism. After being absorbed, it is lost in the intricate processes of nutrition. There is no evidence in favor of the view that oxygen unites directly with carbonaceous matters in the blood which it meets in the lungs, and, by direct union with carbon, forms carbonic acid.

2. How is carbonic acid produced by the system? That carbonic acid makes its appearance in the blood itself, produced in the red corpuscles, has been abundantly proven by observations already cited, although it is impossible to determine to what extent this takes place during life. It is likewise a product of the physiological decomposition of the tissues, whence it is absorbed by the blood circulating in the capillaries and conveyed by the veins to the right side of the heart. It has been experimentally demonstrated that its production is not immediately dependent upon the absorption of oxygen, for its formation continues in an atmosphere of hydrogen or of nitrogen. It is most reasonable to consider the carbonic acid thus formed as a product of excretion or disassimilation, like urea, creatine, or cholesterine. The fact that it may easily be produced artificially, out of the body, does not demonstrate that its formation in the body is as simple as when it is formed by the process of combustion. We may be able at some future time to produce artificially all the excrementitious principles, as has already been done in the case of urea; but we are hardly justified in supposing that the mode of formation of carbonic acid, as one of the phenomena of nutrition, is precisely the same as when it is made by our chemical manipulations.

As expressing nearly all that is known, even at the present day, regarding the mode of formation of carbonic acid in the economy, we may take the following concluding passage from the paper of Collard de Martigny, published in 1830:

"The carbonic acid expired is a product of assimilative decomposition, secreted in the capillaries and excreted by the lungs."

The carbonic acid thus produced is taken up by the blood, part of it in a free state in solution, particularly in the plasma, and a part which has united with the carbonates to form bicarbonates. Carried thus to the lungs, the free gas is removed by simple displacement, and that which exists in combination is set free by the acids found in the pulmonary substance.

3. What is the nature of the intermediate processes, from the disappearance of oxygen to the evolution of carbonic acid? A definite answer to this question would complete our knowledge of the respiratory process; but this, in the present state of the science, we are not prepared to give. We can only repeat what has already been so frequently referred to, that oxygen must be considered as a nutritive principle, and carbonic acid, as a product of excretion. The intermediate processes belong to the general function of nutrition, with the intimate nature of which we are unacquainted. We have not sufficient evidence for supposing that this process is identical with what is generally known as combustion.

The Respiratory Sense, or Want on the part of the System which induces the Respiratory Movements. (*Besoin de respirer.*)

We are all familiar with the peculiar and distressing sense of suffocation which attends an interruption in the respiratory process. Under ordinary conditions, the act of breathing takes place without our knowledge; but even when the air is but little vitiated, when its entrance into the lungs is slightly interfered with or when a considerable portion of the pulmonary structure is involved in disease, we experience a certain sense of uneasiness and become conscious of the necessity of respiratory efforts. This gradually merges into the sense of suffocation, and, if the obstruction be sufficient, is followed by convulsions, insensibility, and finally by death.

Although we are not sensible of any want of air under ordinary conditions, it was proven by the celebrated experiment of Robert Hook, in 1664, that there is a want always felt by the system, and that, if this want be effectually supplied, no respiratory movements will take place. We have often repeated the experiment demonstrating this fact. If a dog be brought completely under the influence of ether, the chest and abdomen opened, and artificial respiration be carefully kept up by means of a bellows fixed in the trachea, even after the animal has come from under the influence of the anæsthetic, so as to look around and wag his tail when spoken to, he will frequently cease all respiratory movements when the air is adequately supplied to the lungs. This fact can be very satisfactorily observed, as the diaphragm and other important respiratory muscles are denuded and exposed to view. If the artificial respiration be interrupted or imperfectly performed, the animal almost immediately feels the want of air, and the exposed respiratory muscles are thrown into violent but ineffectual contraction.

It is generally admitted, indeed, that there exists in the system what may appropriately be regarded as a respiratory sense, or, as it is called by the French, *besoin de respirer*, which is conveyed to the respiratory nervous centre and gives rise to the ordinary reflex and involuntary movements of respiration, that this sense is exaggerated by any thing which interferes with respiration, and is then carried on to the brain, where it is appreciated as dyspnœa and finally as the overpowering sense of suffocation. An exaggeration of the respiratory sense constitutes an oppression, which is referred to the lungs. It has been demonstrated, however, that the sensation of hunger, which is felt in the stomach, and of thirst, which is felt in the throat and fauces, have their seat really in the general system, and are instinctively referred to the parts mentioned, because they are severally relieved by the introduction of food into the stomach and the passage of liquid along the throat and œsophagus. It cannot, therefore, be assumed, from sensations only, that the sense of want of air is really situated in the lungs. The question of its seat and its immediate cause is one of the most interesting of the physiological points connected with respiration.

Many physiologists accept the view of Marshall Hall, that the respiratory sense is located in the lungs, is carried to the medulla oblongata by the pulmonary branches of the pneumogastric nerves, and is due to the accumulation of carbonic acid in the pulmonary vesicles; but there are facts in physiology and pathology which are inconsistent with such an exclusive view.

In cases of disease of the heart, when the system is imperfectly supplied with oxygenated blood, the sense of suffocation is frequently most distressing, although the lungs be unaffected and receive a sufficient supply of pure air. This and other similar facts led Bérard to adopt the view that the respiratory sense has its point of departure in the right cavities of the heart and is due to their distention as the result of obstruction to the passage of blood through the lungs. John Reid thought it was due in a measure to the circulation of venous blood in the medulla oblongata. What has been shown to be the correct explanation was given by Volkmann in 1841. He regarded the sense of want of air as dependent on a deficiency of oxygen in the tissues, producing an impression which is conveyed to the medulla oblongata by the nerves of general sensibility. By a series of experiments, this observer disproved the view that this sense resides in the lungs and is transmitted along the pneumogastric nerves; and, by exclusion, he located it in the general system and showed that such a supposition is sufficient to explain all the phenomena connected with the respiratory movements. In the hope of settling some of these questions, which might be regarded as somewhat uncertain, we instituted, a few years ago, a series of experiments upon the situation and cause of the respiratory sense. In these observations, the following facts, some of which had been previously noted, were demonstrated:

1. If the chest be opened in a living animal, and artificial respiration be carefully performed, inflating the lungs sufficiently but cautiously and taking care to change the air in the bellows every few moments, as long as this is continued, the animal will make no respiratory effort; showing that, for the time, the respiratory sense is abolished.

2. When the artificial respiration is interrupted, the respiratory muscles are thrown into contraction, and the animal makes regular, and at last violent efforts. If we now expose an artery and note the color of the blood as it flows, it will be observed that the respiratory efforts commence only when the blood in the vessel begins to be dark. When artificial respiration is resumed, the respiratory efforts cease only when the blood becomes red in the arteries. The invariable result of this experiment seems to show that the respiratory sense is connected with a supply of blood containing little oxygen and charged with carbonic acid to the systemic capillaries by the arteries, and that it varies in intensity with the degree of change in the blood.

3. If, while artificial respiration is regularly performed, a large artery be opened and the system be thus drained of blood, when the hæmorrhage has proceeded to a certain extent, the animal makes respiratory efforts, which become more and more violent, until they terminate, just before death, in general convulsions. The same result follows when the blood is prevented from getting to the system by applying a ligature to the aorta.

These facts, which may be successively observed in a single experiment, remain precisely the same if we previously divide both pneumogastric nerves in the neck; showing that these are by no means the only nerves which convey the respiratory sense to the medulla oblongata.

The conclusions which may legitimately be drawn from the above-mentioned facts are the following:

The respiratory sense has its seat in the system and is transmitted to the medulla oblongata by the general sensory nerves. It does not originate in the lungs, for it operates when the lungs are regularly filled with pure air, if the system be drained of the oxygen-carrying fluid.

The respiratory sense is due to a want of oxygen on the part of the system, and not to any fancied irritant properties of carbonic acid; for, when the lungs are filled with air, and the system is gradually drained of blood, although all the blood which finds its way to the capillaries is fully oxygenated, as the quantity becomes insufficient to supply the required amount of oxygen, the sense of want of air is felt, and respiratory efforts take place. The experimental results on which these conclusions are based are invariable, and we have demonstrated them repeatedly; so that the location of the respiratory sense in the general system, and the fact that it is an expression of a want of oxygen, seem as certain as that oxygen is taken up by the blood from the lungs and distributed to the tissues by the arteries. With this view we can explain all the reflex phenomena which are connected with the respiratory function.

The supposition of Bérard that the respiratory sense is due to distention of the right cavities of the heart is disproved by the simple experiment of sudden excision of this organ. In that case, as the system is drained of blood, efforts at respiration invariably take place, though the supply of air to the lungs be continued.

Sense of Suffocation.—We must separate, to a certain extent, the respiratory sense from the sense of distress from want of air, and its extreme degree, the sense of suffocation. The first is not a sensation, but an impression conveyed to the medulla oblongata, giving rise to involuntary reflex movements. The necessities for oxygen on the part of the system regulate the supply of air to the lungs. We have already seen that, once in every five to eight respirations, or when the respiratory movements are a little restricted under the influence of depressing emotions, an involuntary deep or sighing inspiration is made, for the purpose of changing the air in the lungs more completely. The increased consumption of oxygen and a certain amount of interference with the mechanical process of respiration during violent muscular exercise put us "out of breath," and for a time the respiratory movements are exaggerated. This is perhaps the first physiological way in which the want of air is appreciated by the senses. A deficiency in hæmatosis, either from a vitiated atmosphere, mechanical obstruction in the air-passages, or grave trouble in the general circulation, produces all grades of sensations, from the slight oppression which is felt in a crowded room, to the intense distress of suffocation. When hæmatosis is but slightly interfered with, only an indefinite sense of oppression is experienced, and the respiratory movements are a little increased, the most marked effect being an increase in the number and extent of sighing inspirations. In the experiments upon animals to which we have referred, when artificial respiration was interrupted, we first noticed regular and not violent contractions of the respiratory muscles; but, as the sense of want of air became exaggerated, every muscle which could be used to raise the chest was brought into action. In the human subject in this condition, the countenance has a peculiar expression of anxiety and distress, and the movements soon extend to the entire muscular system, resulting in general convulsions, and, finally, in insensibility.

Bearing in mind the fact that, although these sensations are referred to the lungs, indicating increased respiratory effort as the common means for their relief, they have their real point of departure in the general system, we can understand the operation of various abnormal conditions of the circulation, when the lungs are adequately supplied with fresh air. The first subjective symptom of air in the veins is a sense of impending suffocation. There is no want of air in the lungs, but the circulation is instantaneously interrupted, and oxygenated blood is not supplied to the tissues. The same effect, practically, follows abstraction of the circulating fluid or the absorption of any poisonous agent which destroys the function of the corpuscles as carriers of oxygen; although, in hæmorrhage, the effects are not so marked, as generally the system is gradually debilitated by the progressive loss of blood. It was invariably noticed, in the experiments above referred to, that, after the division of a large artery, although artificial respiration was carefully performed, respiratory efforts took place when the system became nearly drained of blood. As the hæmorrhage continued, these efforts became more violent and resulted, just before death, in general convulsions. A comparison of this experiment with those in which artificial respiration was simply interrupted shows that, in sudden hæmorrhage, there can be no doubt that the system feels the want of oxygen; and, when the loss of blood is very great, this is increased until it amounts to a sense of suffocation. In gradual hæmorrhage, there is a conservative provision of Nature, by which faintness and diminution in the force of the heart's action favor the arrest of the flow of blood.

Poisoning by carbonic oxide is generally accompanied with convulsions, which arise from the sense of suffocation and are due to a fixation of this gas in the blood-corpuscles, by which they are rendered incapable of carrying oxygen to the system. Convulsions also attend poisoning by hydrocyanic acid, in cases in which the system is not overpowered immediately by a large dose of this agent and the muscular irritability is destroyed.

Experiments have failed to show that the respiratory sense, or the sense of suffocation, is due to irritation produced by carbonic acid in the non-oxygenated blood.

Respiratory Efforts before Birth.

It is generally admitted that one of the most important functions of the placenta, and the one which is most immediately connected with the life of the fœtus, is a respiratory interchange of gases, analogous to that which takes place in the gills of aquatic animals. The vascular prolongations from the fœtus are continually bathed in the blood of the mother, and this is the only way in which it can receive oxygen. Notwithstanding the statements of those who have been unable to note any difference in color between the blood contained in the umbilical arteries and the vein, there are direct observations showing that such a difference does exist. Legallois frequently observed a bright-red color in the blood of the umbilical vein; and, on alternately compressing and releasing the vessel, he saw the blood change in color successively from red to dark and from dark to red. As oxygen is thus adequately supplied to the system, the fœtus is in a condition similar to that of the animals in which artificial respiration was effectually performed. The want of oxygen is fully met, and therefore no respiratory efforts take place. Respiratory movements will take place, however, even in very young animals, when there is a deficiency of oxygen in the system. It has been observed that the liquor amnii occasionally finds its way into the respiratory passages of the fœtus, where it could only enter during efforts at respiration. Winslow, in the latter part of the last century, first noticed respiratory efforts in the fœtuses of cats and dogs in the uterus of the mother during life; and many others have observed that, when fœtuses are removed from vascular connection with the mother, they will make vigorous efforts at respiration. This fact we have frequently had occasion to demonstrate in making operations upon pregnant animals. After the death of the mother, the fœtus always makes a certain number of respiratory efforts, which are not uncertain in their character, but distinct, accompanied by great elevation of the ribs, opening of the mouth, and following each other at regular intervals, independently of irritation of the general surface.

From what has been experimentally demonstrated with regard to the seat and cause of the respiratory sense after birth, it is evident that want of oxygen is the cause of respiratory movements in the fœtus. When the circulation in the maternal portion of the placenta is interrupted from any cause, or when the blood of the fœtus is obstructed in its course to and from the placenta, the impression due to want of oxygen is conveyed to the medulla oblongata, and efforts at respiration are the result. This cannot be due to an accumulation of carbonic acid in the lungs and is entirely consistent with our views, locating the respiratory sense in the general system.

Cutaneous Respiration.

This mode of respiration, although very important in many of the lower orders of animals, is insignificant in the human subject and is even more slight in animals covered with hair or feathers. Still, an appreciable quantity of oxygen is absorbed by the skin of the human subject, and an amount of carbonic acid, which is proportionately larger, is exhaled. Exhalation of carbonic acid, which is connected rather with the functions of the skin as a general eliminating organ and is by no means an essential part of the respiratory process, will be more fully considered under the head of excretion. Carbonic acid is given off with the general emanations from the surface, being found at the same time in solution in the urine and in most of the secretions. It is well known that death follows the application of an impermeable coating to the entire cutaneous surface; but this is by no means due to a suppression of its respiratory function alone. The skin has other offices, particularly in connection with regulation of the animal temperature, which are infinitely more important.

An estimate of the extent of the cutaneous, as compared with pulmonary respiration, has been made by Scharling, by comparing the relative quantities of carbonic acid exhaled in the twenty-four hours. According to this observer, the skin performs from $\frac{1}{50}$ to $\frac{1}{40}$ of the respiratory function. It is exceedingly difficult to collect all the carbonic acid given off by the skin under perfectly normal conditions. In some recent observations by Aubert, the estimate is very much lower than that given by Scharling.

Asphyxia.

The effects of cutting off the supply of oxygen from the lungs are mainly referable to the circulatory system and have already been considered under the head of the influence of respiration upon the circulation. It will be remembered that, in asphyxia the non-aërated blood passes with so much difficulty through the systemic capillaries as finally to arrest the action of the heart. It is the experience of those who have experimented on this subject, that the movements of the heart, once arrested in this way, cannot be restored, but that while the slightest regular movements continue, its functions will gradually return if air be readmitted to the lungs.

A remarkable power of resisting asphyxia exists in newly-born animals that have never breathed. This was noticed by Haller and others and has been the subject of numerous experiments, among which we may mention those of Buffon, Legallois, and W. F. Edwards. Legallois found that young rabbits would live for fifteen minutes deprived of air by submersion, but that this power of resistance diminished rapidly with age. W. F. Edwards has shown that there exists a great difference in this regard in different classes of animals. Dogs and cats, which are born with the eyes shut and in which there is at first a very slight development of animal heat, will show signs of life after submersion for more than half an hour; while Guinea-pigs, which are born with the eyes open, are much more active, and produce a greater amount of heat, will not live more than seven minutes. The cause of this peculiarity has been attributed to the existence of the foramen ovale, enabling the blood to get to the system without passing through the lungs, by those who regard the arrest of the circulation in asphyxia as due to obstruction to the pulmonary circulation; but this explanation is not sufficient, as blood passes easily through the lungs in asphyxia and is obstructed only in the systemic capillaries. The true explanation seems to be that, in most warm-blooded animals, during the very first periods of extra-uterine life, the demands on the part of the system for oxygen are comparatively slight. At this time, there is very little activity in the processes of nutrition, and the actual consumption of oxygen and exhalation of carbonic acid are much below the usual regular standard in animals of this class. In fact, their condition is somewhat like that of cold-blooded animals. The actual difference in the consumption of oxygen immediately after birth and at the age of a few days is sufficient to explain the remarkable power of resisting asphyxia just after birth.

One of the most interesting questions, in a practical point of view, connected with the subject of asphyxia, is the effect on the system of air vitiated from breathing in a confined space. There are here several points which present themselves for consideration. The effect of respiration on the air is to take away a certain proportion of oxygen and to add certain principles which are regarded as deleterious. The emanation which is generally regarded as having the most decided influence upon the system is carbonic acid. A careful review of the most reliable observations on this subject shows that the influence of carbonic acid is generally very much over-estimated. In poisoning by charcoal-fumes, it is generally carbonic oxide which is the active principle. Regnault and Reiset exposed dogs and rabbits for many hours to an atmosphere containing twenty-three parts per hundred of carbonic acid artificially introduced, and thirty to forty parts of oxygen, without any ill effects. They took care, however, to keep up a constant supply of oxygen. These experiments are at variance with the results obtained by others, but Regnault and Reiset explain this difference by the supposition that the gases in other observations were probably impure, containing a little chlorine or carbonic oxide. There is no reason to doubt, from the high reputation of these observers for skill and accuracy, that their experiments are perfectly reliable; and, in that case, they prove that carbonic acid does not act upon the system as a poison. This view is sustained by the observations of Bernard with carbonic oxide, which is known to be excessively poisonous. In animals killed by this gas, the blood, both venous and arterial, is of a bright-red color, which is due to the fixation of the gas by the blood-corpuscles. In this way, the red corpuscles, which act normally as respiratory agents carrying oxygen to the tissues, are paralyzed, and the animal dies from asphyxia. We have already referred to this remarkable affinity of the red corpuscles for carbonic oxide and its action in arresting the transformation of oxygen into carbonic acid in the blood, in treating of the different methods of analysis of the blood for gases, and have shown that this gas is the proper agent to use in the method of analysis by displacement.

In breathing in a confined space, the distress and the fatal results are produced, in all probability, more by animal emanations and a deficiency of oxygen than by the presence of carbonic acid. When the latter gas is removed as fast as it is produced, the effects of diminution in the proportion of oxygen are soon very marked, and they progressively increase until death occurs. Bernard has shown that birds enclosed in a confined space, from which the carbonic acid is carefully removed, will gradually consume oxygen, until, when death occurs, the proportion is reduced to from three to five parts per hundred. When the carbonic acid is allowed to remain, the increased density of the atmosphere interferes with the diffusion between the gases of the blood and the air, and death supervenes with greater rapidity.

The influence on animals of emanations from the lungs and general surface is undoubtedly very considerable; and this fact, which almost all have experienced more or less, has been fully and painfully illustrated in several instances of large numbers of persons confined without proper change of air. Overcrowding is one of the most prolific sources of disease among the poorer classes of society; and there are many forms of disease prevalent in large cities, that are almost unknown in the rural districts and that can be alleviated only by proper sanitary regulations, which, unfortunately, are often very difficult to enforce.

In crowded assemblages, the slight diminution of oxygen, the elevation of temperature, increase in moisture, and particularly the presence of organic emanations, combine to produce unpleasant sensations. The terrible effects of this carried to an extreme degree were exemplified in the confinement of the one hundred and forty-six English prisoners, for eight hours only, in the "Black Hole" of Calcutta, a chamber eighteen feet square, with only two small windows, and those obstructed by a veranda. Out of this number, ninety-six died in six hours, and one hundred-and twenty-three, at the end of the eight hours. Many of those who immediately survived died afterward of putrid fever. This frightful tragedy has frequently been repeated on emigrant and slave ships, by confining great numbers in the hold of the vessel, where they were entirely shut out from the fresh air. This subject possesses great pathological interest; the effects of an insufficient supply of air and the accumulation in the atmosphere of animal emanations being very important in connection with the cause and prevention of many diseases.

The condition of the system has a marked and important influence on the rapidity with which the effects of vitiated atmosphere are manifested, as we should anticipate from what we know of the variations in the consumption of oxygen under different conditions. As a rule, the immediate effects of confined air are not so rapidly manifested in weak and debilitated persons as in those who are active and powerful. It has sometimes been observed, in cases where a male and female have attempted suicide together by the fumes of charcoal, that the female may be restored some time after life is extinct in the male. This is probably owing to the greater demand for oxygen on the part of the male.

The following interesting fact is reported by Bernard, showing the relative power of resisting asphyxia in health and disease:

"Two young persons were in a chamber warmed by a stove fed with coke. One of them was seized with asphyxia and fell unconscious. The other, at that time suffering with typhoid fever and confined to the bed, resisted sufficiently to be able to call for help. We know already that this resistance to toxic influences is manifested in animals, when they are made sick; we here have the proof of the same phenomenon in man. As for the one who, in good health, had experienced the effects of the commencement of poisoning, she had a paralysis of the left arm, which was not completely cured at the end of six months."

When poisoning by confined air is gradual, the system becomes somewhat accustomed to the toxic influence, the temperature of the body is lowered, and an animal will live in an atmosphere which will produce instantaneous death in one that is fresh and vigorous. Bernard has made a number of curious and instructive experiments on this point. In one of them a sparrow was confined under a bell-glass for one hour and a half, at the end of which time another was introduced, the first being still quite vigorous. The second became instantly much distressed and died in five minutes; but, ten minutes after, the sparrow which had been confined for more than an hour and a half was released and flew away. The points to which we have alluded have been confirmed and the observations somewhat extended by the more recent researches of Bert. This is simply demonstrating, with experimental accuracy, a fact of which we are all conscious; for it is well known that, going from the fresh air into a close room, we experience a *malaise* which is not felt by those who have been in the room for a length of time and whose emanations have vitiated the atmosphere.

CHAPTER VI.

ALIMENTATION.

Appetite—Circumstances which modify the appetite—Influence of habit—Hunger—Seat of the sense of hunger—Thirst—Seat of the sense of thirst—Duration of life in inanition—Division of alimentary principles—Nitrogenized alimentary principles—Non-nitrogenized alimentary principles—Inorganic alimentary principles—Water—Alcohol—Distilled liquors—Wines, malt liquors, etc.—Coffee—Tea—Chocolate—Condiments and flavoring articles—Quantity and variety of food necessary to nutrition—Necessity of a varied diet.

In the organism of animals, every part is continually undergoing what may be called physiological decay; the organic nitrogenized principles are being constantly transformed into effete matter; and, as these constituents never exist without inorganic principles, with which they are closely and inseparably united, it is found that the products of their decay are always discharged from the body in combination with inorganic matters. This process of molecular change is a necessary and an inevitable condition of life. Its activity may be increased or retarded by various means, but it cannot be arrested. The excrementitious principles which are thus formed are produced constantly by the tissues and must be continually removed from the organism, otherwise they accumulate and induce serious toxic conditions. Examples of this are found in those diseases of the kidneys which interfere with the elimination of urea, producing uræmic poisoning, and in diseases of the liver which interfere with the elimination of cholesterine, giving rise to cholesteræmia.

It is evident, from the amount of matter that is daily discharged from the body, that the process of disassimilation, as it is called, must be very active. Its constant operation necessitates a constant appropriation of new matter by the parts, in order that they may maintain their integrity of composition and be always ready to perform their functions in the economy. The blood contains all the principles necessary for the regeneration of the organism. Its inorganic constituents are generally found in the form in which they exist in the substance of the tissues; but the organic principles of the parts are formed in the substance of the tissues themselves, by a transformation of material furnished by the blood. The physiological decay of the organism is, therefore, being constantly repaired by the blood; but, in order to keep the great nutritive fluid from becoming impoverished, the materials which it is constantly losing must be supplied from some source out of the body, and this necessitates the ingestion of matters which are known as food. Food is taken into the body in obedience to a want on the part of the system, which is expressed by the sensation of hunger, when it relates to solid or semi-solid matters, and thirst, when it relates to water. As these sensations constitute the first cause of the introduction of materials capable of regenerating the blood, their consideration naturally precedes the study of digestion, the process by which the articles of food are prepared for absorption and appropriation by the circulating fluid.

Hunger and Thirst.

The term hunger may be applied to all degrees of that peculiar want felt by the system which induces the ingestion of nutritive principles. Its first manifestations are, perhaps, best expressed by the term appetite; a sensation by no means disagreeable, and one which may be excited by the sight, smell, or even the recollection of savory articles, at times when it does not absolutely depend on a want in the system. In the ordinary and moderate development of the appetite, it is impossible to say that the sensation is referable to any distinct part or organ. It is influenced in some degree by habit; in many persons, the feeling being experienced at or near the hours when food is ordinarily taken. If not soon gratified, the appetite is rapidly intensified until it becomes actual hunger. Except when the quantity of food taken is unnecessarily large, the appetite simply disappears on the introduction of food into the stomach and gives place to the sense of satisfaction which accompanies the undisturbed and normal action of the digestive organs; or, in those who are in the habit of engaging in absorbing occupations at that time, the only change experienced is the absence of desire for food. The sense of oppression and fulness which attends over-distention of the stomach is simply superadded to the feeling of satisfaction of the appetite, of which it is not a necessary part.

In man, the appetite is usually manifested in a marked degree at least twice, and generally three times in the twenty-four hours. In this country, food is commonly taken three times daily. In childhood, when the system demands material, not only for the repair of worn-out parts but for growth, food is generally taken oftener and in larger relative quantity than in the adult. The infant should satisfy the appetite at least six or seven times in the twenty-four hours; and nothing has a more serious influence upon the development of the growing child than bad quality or a restricted quantity of food.

It has been observed that children and old persons do not endure deprivation of food so well as adults. This fact was noted by M. Savigny, in the case of the wreck of the frigate Medusa. After the wreck, one hundred and fifty persons, of all ages, were exposed on a raft for thirteen days with hardly any food. Out of this number only fifteen survived, among them M. Savigny; and the children, young persons, and the aged, were the first to succumb.

Important modifications in the appetite are due to temperature. In cold climates, and during the winter season in all climates, the desire for food is notably increased, and the tastes are somewhat modified. Animal food, and particularly fats, are more agreeable at that time, and the quantity of nutriment which is demanded by the system is then considerably greater. In many persons, the difference in the appetite in warm and cold seasons is very marked.

Exercise and occupation, both mental and physical, when not pushed to the point of exhaustion, increase the desire for food and undoubtedly facilitate digestion. Certain articles, especially the vegetable bitters, taken into the stomach immediately before the time when food is habitually taken, frequently have the same effect; while other articles, which do not satisfy the requirements of the system, have a tendency to diminish the desire for food. Many articles of the materia medica, especially preparations of opium, have, in some persons, a marked influence in diminishing the appetite. The abuse of alcoholic stimulants will sometimes take away all desire for food. When hunger is pressing, it has been observed that tobacco, in those who are accustomed to its use, will frequently allay the sensation for a time. When the system has been badly nourished from any cause, as after prolonged abstinence or in recovery from an exhausting disease, hunger is generally pressing and almost constant; and this continues until the organism has regained its normal condition. Under these circumstances, the ingestion of food, even in unusually large quantity, has but a momentary effect in appeasing the appetite; showing that, although the feeling of satiety which follows the introduction of a sufficient quantity of food into the stomach is experienced, the system still feels the want of nourishment, and this want is expressed by an almost immediate recurrence of the appetite.

If food be not taken in obedience to the demands of the system as expressed by the appetite, the sensation of hunger becomes most distressing. It is then manifested by a peculiar and indescribable sensation in the stomach, which soon becomes developed into actual pain. This is generally accompanied by intense pain in the head and a feeling of general distress, which soon render the satisfaction of this imperative demand on the part of the system the absorbing idea of existence. Starvation overcomes, in many instances, every moral and intellectual feeling and gives full play to the purely animal instincts. Furious delirium frequently supervenes after a few days of complete abstinence; and this is generally the immediate precursor of death. It is unnecessary to cite any of the numerous instances in which murder and cannibalism are resorted to when starvation is imminent; suffice it to say, that the extremity of hunger or of thirst, like the sense of impending suffocation, is a demand on the part of the system so imperative, that it must be satisfied if within the range of possibility. There have been instances of sublime resignation in the face of this terrible agony, but these are rare in comparison with the examples of frightful expedients to satisfy the demands of Nature.

The question of the seat of the sense of hunger is one of considerable physiological interest. When we say that it is instinctively referred to the stomach, it is simply expressing the fact that the sensation is of a nature to demand the introduction of food into the alimentary canal. The sense of the want of air demands the introduction of fresh air into the lungs; but, though air be inspired, if any thing interfere with its passage to the system by the blood, the demand for oxygen is unsatisfied. It has been shown that the real seat of the respiratory sense is in the general system, and that this is referred to the lungs because it is necessarily by the introduction of air into these organs that the want is met. The same principle is manifested, in a manner no less distinct, with regard to the ingestion and assimilation of food. When the system is suffering from defective nutrition, as after prolonged abstinence or during recovery from diseases which have been accompanied by lack of assimilation, the mere filling of the stomach produces a sensation of repletion of this organ, but the sense of hunger is not relieved; but if, on the other hand, the nutrition be active and sufficient, the stomach is frequently entirely empty for a considerable time without the development of the sense of hunger. The following observation bears strongly on this point: In a dog with a fistula into the gall-bladder, the bile-duct having been tied and partly exsected, digestion was so much interfered with that death from inanition took place in thirty-eight days; and, although the animal took food abundantly, the appetite was voracious and never satisfied. The same phenomenon has sometimes been observed in cases of diabetes accompanied with great deficiency of assimilation. The appetite is preserved and hunger is felt by persons who suffer from extensive organic disease of the stomach, and the sensation has been occasionally relieved by nutritious enemata or by injections into the veins.

An interesting and curious case has been reported by Prof. Busch, of Bonn, which points almost conclusively to a want of assimilation of nutritive matter by the general system as the main cause of the sensation of hunger. In this case, which will be more fully detailed hereafter, there existed a fistula into what appeared to be the upper third of the small intestine. The patient was a woman, thirty-one years of age, who, in the sixth month of her fourth pregnancy, received the injury which resulted in the fistulous opening, by being tossed by a bull, one of the horns penetrating the abdomen. She was seen by Prof. Busch six weeks after the injury, at which time every thing taken into the stomach passed at the upper opening of the fistula. Although the patient took food in large quantity, she became extremely emaciated and weak. "The patient at first had a most voracious appetite; she never felt satisfied. She continued to eat, even when the first portions of food which she had taken were escaping through the opening. She would then say that she felt better, but was still hungry. Prof. Busch infers that hunger is composed of two separate sensations—one general, the other local; the former resulting from the want of material to supply the waste of tissue." Such facts render it certain that the appetite and the sense of hunger are expressions of a general want on the part of the system, referred by our sensations to the stomach, but really located in the general system. This want can only be completely satisfied by the absorption of digested alimentary matter by the blood and its assimilation by the tissues.

The sense of hunger is undoubtedly appreciated by the cerebrum, and it has been a question whether there be any special nerves which have the function of conveying this impression to the great nervous centre. The nerve which would naturally be supposed to possess this function is the pneumogastric; but, notwithstanding certain observations to the contrary, it has been proven that section of both of these nerves by no means abolishes the desire for food. Longet has observed that dogs eat, apparently with satisfaction, after section of the glosso-pharyngeal and lingual nerves. This observer is of the opinion that the sensation of hunger is conveyed to the brain through the sympathetic system. Although there are various considerations which render this somewhat probable, it is not apparent how it could be demonstrated experimentally. It is undoubtedly the sympathetic system of nerves which presides specially over nutrition; and hunger, which depends upon deficiency of nutrition, is certainly not conveyed to the brain by any of the cerebro-spinal nerves.

Thirst is the special sensation which induces the ingestion of water. In its moderate development, this is usually an indefinite feeling, accompanied with more or less sense of dryness and heat of the throat and fauces, and sometimes, after the ingestion of a quantity of very dry food, by a peculiar sensation referred to the stomach. When the sensation of thirst has become intense, the immediate satisfaction which follows the ingestion of a liquid, particularly water, is very great. Thirst is very much under the influence of habit, some persons experiencing a desire to take liquids only two or three times daily, while others do so much more frequently. The sensation is also sensibly influenced by the condition of the atmosphere, as regards moisture, by exercise, and by other circumstances which influence the discharge of water from the body, particularly by the skin. A copious loss of blood is always followed by great thirst. This we have frequently noticed in the inferior animals. After an operation involving hæmorrhage, they nearly always drink with avidity as soon as released. In diseases which are characterized by increased discharge of liquids, thirst is generally excessive.

The demand on the part of the system for water is much more imperative than for solids; in this respect being only second to the demand for oxygen. Animals will live much longer deprived of solid food but allowed to drink freely than if deprived of both food and drink. A man, supplied with dry food but deprived of water, will not survive more than a few days. Water is necessary to the function of nutrition, and acts, moreover, as a solvent in removing from the system the products of disassimilation.

After deprivation of water for a considerable time, the intense thirst becomes most agonizing. The dryness and heat of the throat and fauces are increased and accompanied by a distressing sense of constriction. A general febrile condition supervenes, the blood is diminished in quantity and becomes thickened, the urine is scanty and scalding, and there seems to be a condition of the principal viscera approaching inflammation. Death takes place in a few days, generally preceded by delirium.

The sensation of thirst is instinctively referred to the mouth, throat, and fauces; but it is not necessarily appeased by the passage of water over these parts, and it may be effectually relieved by the introduction of water into the system by other channels, as by injecting it into the veins. Bernard has demonstrated, by the following experiment, that water must be absorbed before the demands of the system can be satisfied: He made an opening into the œsophagus of a horse, tied the lower portion, and allowed the animal to drink after he had been deprived of water for a number of hours. The animal drank an immense quantity, but the water did not pass into the stomach, and the thirst was not relieved. He modified this experiment by causing dogs to drink with a fistulous opening into the stomach by which the water was immediately discharged. They continued to drink without being satisfied, until the fistula was closed and the water could be absorbed. We have often repeated the latter experiment in public demonstrations. In one of these particularly, the animal drank repeatedly until he had taken several quarts of water, only ceasing from fatigue and soon recommencing; but, so soon as the fistula was closed, he drank a moderate quantity and was satisfied.

In a case reported by Dr. Gairdner, of Edinburgh, in the human subject, all the liquids swallowed passed out at a wound in the neck by which the œsophagus had been cut across. The thirst in this case was insatiable, although buckets-full of water were taken in the day; but, on injecting water, mixed with a little spirit, into the stomach, the sensation was soon relieved. This observation was made in 1820, long before the experiments just referred to upon the inferior animals.

Although the sensation of thirst is referred to special parts, it is an expression of the want of fluids in the system and is to be effectually relieved only by the absorption of fluids by the blood. There are no nerves belonging to the cerebro-spinal system which have the office of carrying this sensation to the brain, division of which will abolish the desire for liquids. Experiments show that no effectual relief of the sensation is afforded by simply moistening the parts to which the heat and dryness are referred. As a demand on the part of the system, it is entirely analogous to the sense of want of air and of hunger, differing only in the way in which it is manifested.

After a certain period of inanition, febrile movement and general agitation occur, and there is almost always disturbance of the mental faculties, amounting sometimes to furious delirium. Frequently, however, the delirium is of a mild character, with hallucinations. There are cases in which there is no marked mental disturbance, but these are generally in persons who voluntarily suffer starvation.

The length of time that life continues after complete deprivation of food and drink is very variable. The influences of age and obesity have already been referred to. Without citing the numerous individual instances of starvation in the human subject which have been reported, it may be stated, in general terms, that death occurs after from five to eight days of total deprivation of food. In 1816, one hundred and fifty persons, wrecked on the frigate Medusa, were exposed on a raft in the open sea for thirteen days. At the end of this time only fifteen were found alive. One of the survivors, M. Savigny, gave, in an inaugural thesis, a very instructive and accurate account of this occurrence, which has been very generally quoted in works of physiology. Authentic instances are on record in which life has been prolonged much beyond the period above mentioned; but they generally occurred in persons who were so situated as not to suffer from cold, which the system, under this condition, has very little power to resist. In these cases, also, there was no muscular exertion, and water was generally taken in abundance. All of these circumstances have an important influence in prolonging life.

Bérard quotes the example of a convict who died of starvation after sixty-three days, but in this case water was taken. An instance of eight miners who survived after five days and sixteen hours of almost complete deprivation of food is referred to in works upon physiology. Bérard also quotes from various authorities instances of deprivation of food for periods varying from four months to sixteen years. All of the subjects were females, and the histories of such cases, reports of which are by no means uncommon, belong properly to psychology, as they undoubtedly are examples of that morbid desire to excite sympathy and interest, which is sometimes observed and which leads to the most adroit and persevering efforts at deception.

From thirty to thirty-five days may be taken as the average duration of life in dogs deprived entirely of food and drink. This fact it is important to bear in mind in connection with observations on the nutritive value of different articles of food.

Alimentation.

Under the name of aliment, in its widest signification, it is proposed to include all articles composed of or containing elements in a form which enables them to be used for the nourishment of the body, either by being themselves appropriated by the organism, by influencing favorably the process of nutrition, or by retarding disassimilation. Those principles which are themselves appropriated may be called direct aliments; and those which simply assist nutrition without contributing reparative material, together with those which retard disassimilation, may be termed accessory aliments. By this definition of aliment, nothing is excluded which contributes to nutrition. The air must be considered in this light, as well as water and all articles which are commonly called drinks.

In the various articles used as food, nutritious elements are frequently combined with each other and with indigestible and non-nutritious matters. The elements of the food which are directly used in nutrition are the true alimentary principles, embracing, thus, only those principles which are capable of absorption and assimilation. The ordinary food of the warm-blooded animals contains alimentary principles united with innutritious substances from which they are separated in digestion. This necessitates a complicated digestive apparatus. In some of the inferior animals, the quantity of nutritious material forms so small a part of the food that the digestive apparatus is even more complicated than in the human subject. This is especially marked in the herbivora, the flesh of which forms an important part of the diet of man. In addition to what are distinctly recognized as alimentary principles, food contains many substances having an important influence on nutrition, which have never been isolated and analyzed, but which render it agreeable. Many of these principles are developed in the process of cooking. They will be considered, as far as practicable, in connection with the different articles of diet.

The alimentary principles belong to the inorganic, vegetable, and animal kingdoms, and are generally divided into the following classes:

1. Organic nitrogenized principles (albumen, fibrin, caseine, musculine, etc.), belonging to the animal kingdom, and vegetable nitrogenized principles, such as gluten and legumine.
2. Organic non-nitrogenized principles (sugars, fats, and starch).
3. Inorganic principles.

Nitrogenized Alimentary Principles.

In the nutrition of certain classes of animals, these principles are derived exclusively from the animal kingdom, and in others, exclusively from the vegetable kingdom; but in man, who is omnivorous, both animals and vegetables contribute nitrogenized material. In both animal and vegetable food, these principles are always found combined with inorganic matters (water, chloride of sodium, the phosphates, sulphates, etc.), and frequently with non-nitrogenized principles (sugar, starch, and fat).

Musculine.—Of the different nitrogenized principles used as food, musculine, albumen, caseine, and fibrin are the most important. Musculine, the organic principle which forms the bulk of the muscular substance, is perhaps the most important and abundant article of this class. This substance is always united with more or less inorganic matter, which cannot be separated without incineration. The flesh of different animals presents wide differences in general appearance, in nutritive properties, and in flavor, which become more marked after the formation of the odorous, empyreumatic substances which are developed in cooking; but the organic principle of all of them is musculine. Muscular tissue is rendered much more digestible by cooking, a process which serves to disintegrate, to a certain extent, the intermuscular areolar tissue and facilitates the action of the digestive fluids. The savors developed in this process have a decidedly favorable influence on the secretion of the gastric juice. It is doubtful whether pure musculine would be capable of supporting life for a long period; but the muscular tissue has been shown by experiment to be sufficient for the purposes of nutrition, in the carnivora, and it undoubtedly is in man.

Of all kinds of muscular tissue, beef possesses the greatest nutritive power. Other varieties of flesh, even that of birds, fishes, and animals in a wild state, do not present an appreciable difference, as far as can be ascertained by chemical analysis; but when taken daily for a long time, they become distasteful, the appetite fails, and the system seems to demand a change of diet. The flesh of carnivorous animals is rarely used as food; and animals that feed upon animal as well as vegetable food, such as pigs or ducks, acquire a disagreeable flavor when the diet is not strictly vegetable.

Albumen.—This is an alimentary principle hardly second in importance to musculine. As an article of diet, it is chiefly found in the white of egg, where it exists in great quantity and is combined with a variety of inorganic substances. Although an important alimentary principle, it cannot meet all the nutritive requirements of the organism. Numerous observations on the inferior animals have shown that pure albumen will not sustain life. The egg of the fowl, however, containing, in addition to albumen, a large quantity of inorganic matter, the fatty matter of the yolk, and other organic principles, is a most nutritious article of food. The albuminoid matters constitute the great nutritive nitrogenized principles of the blood and are the substances into which all the principles of this class which exist in food are converted before they are applied to the nutrition of the tissues.

Caseine.—At a certain period of life, caseine constitutes essentially the sole nitrogenized article of food. It is found only in milk, and it exists largely in the great variety of cheeses, which are manufactured from milk. In addition to caseine, milk contains butter, sugar, and a variety of inorganic principles. Milk is capable of supplying material for the nourishment of all parts of the organism, caseine furnishing the nitrogenized principle. In the form of cheese, caseine constitutes an important article of food.

Fibrin.—Fibrin is by no means so important an article of diet as those just considered, and it very seldom forms any considerable part of our food The same may be said of some other principles of this class, such as globuline, which is the organic principle of the blood-corpuscles, vitelline, a principle peculiar to the yolk of the egg, osteine and cartilagine. The last two substances are generally taken after they have undergone peculiar modifications in cooking, when they are known by other names.

Gelatine and Chondrine, etc.—After prolonged boiling, the organic principles of the bones, integuments, areolar tissue, tendons, and other structures composed of the white fibrous tissue, are dissolved and transformed into a new substance which is called gelatine. Cartilage treated in the same way is in great part converted into chondrine. The principles thus formed are soluble in hot water, rendering it slightly viscid, but on cooling the whole mass becomes of a more or less gelatinous consistence, according to the quantity of gelatine that is present. A considerable quantity of inorganic matter, particularly phosphate of lime, is always present in combination with gelatine.

Gelatine and chondrine present slight differences as regards their chemical reactions, in other respects being nearly identical. The sulphate of alumina, alum, and the sulphate of iron, will precipitate chondrine but have no influence on a solution of gelatine. Tannin, or infusion of galls, added to a solution of gelatine, produces a brownish precipitate. This reaction is marked in a solution containing but one part of gelatine to five thousand parts of water. Both gelatine and chondrine are of indefinite chemical composition and uncrystallizable. By the action of sulphuric acid, gelatine is transformed into a crystallizable substance called glycocolle, which has a sweetish taste, is soluble in water, and is insoluble in alcohol and ether. According to some, this is capable of being separated into alcohol and carbonic acid by fermentation.

A great deal of interest was at one time attached to gelatine as an article of food, from the fact that it is formed and extracted from parts, particularly the bones, which were before regarded as comparatively useless. Indeed, the experiment of diminishing the quantity of meat and supplying in its place the extract of bones was made in several hospitals and manufacturing establishments in France; but this change in diet led so universally to complaints of insufficiency of food, that experiments were soon instituted with a view of determining whether gelatine really possessed any nutritive power. Without entering into a full discussion of these experiments, it may be stated that the introduction of gelatine as an article of diet, to the exclusion of other principles which were known to be nutritive, was always followed by loss of weight and the indications of more or less defective nutrition. In other words, the introduction of gelatine did not permit any diminution in the quantity of ordinary articles of food. The whole question was finally settled by the researches of Magendie, the reporter of the French committee on gelatine, in 1841. This report embodied the results of numerous experiments on the effects of various nitrogenized principles, but the conclusions with regard to gelatine were very striking. When taken alone, it was distasteful in the highest degree, even to animals on the verge of starvation; even the agreeable jelly formed of different parts of the pig and the giblets of fowl, prepared by the *charcutiers* of Paris, which were at first taken by the animals with apparent satisfaction, was refused after a few days; and, when animals were confined exclusively to this article, death took place about the twentieth day, with all the symptoms of inanition.

The flavor of meat was formerly supposed to depend chiefly on a peculiar principle, called, by Thénard, osmazome. This name is now seldom used, as the substance which was so called is known to be composed of various empyreumatic nitrogenized products, with lactic acid, the lactate of soda, the inosate of potash, creatine, creatinine, and other principles the nature of which has not been determined.

Most of the vegetable articles of food contain more or less nitrogenized matters which resemble very closely their analogues in the animal kingdom. Some of these vegetable principles resemble those above considered so closely that they have been called respectively, vegetable albumen, fibrin, and caseine. They all, however, present certain distinguishing peculiarities.

Vegetable Albumen.—In the juice of most vegetables which are used as food, there exists a substance, coagulable by heat and by alcohol, and having the same composition as ordinary albumen with the exception of the equivalents of phosphorus and sulphur. This is found most abundantly in the juice of turnips, carrots, cabbages, and vegetables of this class. In wheaten flour, which contains nearly all classes of alimentary principles, it is also found, but in small quantity.

There is every reason to suppose that, as nutritive principles, vegetable and animal albumen are nearly identical. Many of the largest and strongest animals are nourished exclusively from the vegetable kingdom. The human subject and many of the inferior animals may be nourished at will by vegetable or by animal food. There is, however, always a physiological difference in the various nitrogenized principles, which is not appreciable by chemical analysis. The flesh of the carnivora, when used as food, is not the same as the flesh of the herbivora; and the quality of the meat may be modified in many animals by changing them from vegetable to animal food. Although the muscular tissue of one animal may be used for the nourishment of another, the flesh of an animal thus nourished is not an appropriate food for man. We should live upon vegetable principles; taking them in part directly, and in part indirectly, or after they have been prepared and assimilated by animals. As a rule, the nutritive principles in vegetables are relatively less abundant than in animal food, and the indigestible residue is therefore greater; but man, and even the carnivorous animals, may be nourished for an indefinite period by appropriate articles derived from the vegetable kingdom.

Vegetable Fibrin and Caseine.—Many of the vegetable juices contain a spontaneously-coagulable substance which has been called vegetable fibrin. This is particularly abundant in the cereals. What has been said concerning fibrin as an alimentary principle is applicable to this substance. Its proportion in vegetables is small, unless we consider as vegetable fibrin, gluten, one of the most abundant and important of the nutritive principles contained in ordinary flour.

A principle may be extracted from beans, peas, and other vegetables of this class, which is thought by many to be identical, in all respects, with caseine and has been called vegetable caseine. The article called *tao-foo*, made by the Chinese from peas, is apparently identical with cheese. The peas are reduced to a pulp by boiling and the vegetable caseine is coagulated by rennet,being afterward treated in the same way as the analogous substance manufactured from milk. Vegetable and animal caseine have, as far as we know, identical physiological relations. Vegetable caseine is sometimes called legumine. It is sparingly soluble in water, is insoluble in alcohol, is not coagulated by heat, and is precipitated by the mineral acids and some of the mercurial and calcareous salts. It is dissolved by the vegetable acids.

Another substance, supposed by some to be identical with vegetable caseine, is amandine. This is found widely distributed in the vegetable kingdom, but it hardly presents points of distinction from legumine, sufficient to mark it as a distinct principle.

Gluten.—In many of the vegetable grains known as cereals, there exists, in variable proportions, a highly-nutritive nitrogenized substance called gluten. This is found in great abundance (from ten to thirty-five per cent.) in wheat. Its proportion in other grains is insignificant. It may be easily extracted from ordinary wheaten flour, by kneading under a stream of water, when the starch, a little sugar, vegetable albumen, mucilage, and some soluble matters are removed, and the gluten remains in the form of an adhesive, elastic, grayish-white mass. Gluten is capable of acting as a ferment, transforming starch first into dextrine and then into sugar. It is the substance which gives the peculiar consistence and porous character to bread.

The nutritive power of gluten is so great, and it contains such a variety of alimentary principles, that dogs are well nourished and can live indefinitely on it when taken as the sole article of food. This experiment was actually made by the gelatine committee; and the fact will be easily understood when we consider that it is a compound of no less than three distinct nitrogenized principles, together with fatty and inorganic matters. In one of the methods of treatment of diabetes mellitus, in which all saccharine and amylaceous matters are excluded from the food, it has been found difficult to nourish the body sufficiently and give proper variety to the diet without bread; and, under these circumstances, the use of bread composed almost exclusively of gluten has been highly successful. With proper care, a bread can be made in this way, which is eminently nutritive and not unpalatable.

Gluten obtained by washing flour under a stream of water contains vegetable fibrin, vegetable albumen, and a substance soluble in alcohol, called glutine. This latter substance is found in quantity only in wheaten flour.

In the different articles of food belonging to the vegetable kingdom, there are undoubtedly many nitrogenized matters with the distinguishing properties of which we are not yet familiar. In their relations to the body as alimentary principles, these would not possess much practical interest, even if they had all been isolated and studied; for all articles of this class are apparently transformed into the same nutritive principles, namely, the albuminoid constituents of the blood.

Non-Nitrogenized Alimentary Principles.

The important principles belonging to the class of non-nitrogenized matters are the sugars, starch, and fat. From the fact that these are supposed by some to be exclusively concerned in keeping up the animal temperature by the oxidation of carbon, they are frequently spoken of as the carbonaceous or calorific elements of food. They are sometimes called hydro-carbons.[1]

In many respects there are marked and important differences between the nitrogenized and non-nitrogenized articles of food; and whether or not these differences relate to the nutrition of the organism is a question which will be considered in its appropriate place. The production of animal heat, which is supposed by some to be due entirely to the action of non-nitrogenized substances, is closely connected with the function of nutrition, and all that is at present known of this general process must be taken into consideration in connection with calorification. It is certain, however, that all alimentary and proximate principles which contain nitrogen, excluding the inorganic and some crystallizable organic substances, have very different properties from those which contain no nitrogen. While the nitrogenized principles are in a state of continual change, so that it is impossible to fix upon any formula as representing their exact ultimate composition, the non-nitrogenized principles are not changed, unless by the influence of some other substance known as a ferment, and have a distinct and definite chemical composition. The latter not only differ greatly from the nitrogenized principles, but most of the individual articles of this class present distinctive peculiarities in their general properties, reactions, and ultimate composition. Treating of them as alimentary principles, we have now only to do with their general properties and the changes which they may be made to undergo out of the body.

Sugar.—A great many varieties of sugar occur in food, and this principle may be derived from both the animal and the vegetable kingdom. The most common varieties derived from animals are sugar of milk, and honey, beside a small quantity of liver-sugar, which is taken whenever the liver is used for food. The sugars derived from the vegetable kingdom are cane-sugar, under which head may be classed all varieties of sugar except that obtained from fruits, and grape-sugar, which comprises all the varieties existing in fruits. In addition, an impure, uncrystallizable residue, obtained in the manufacture of the different varieties of cane-sugar, called molasses, is a common article of food. The following are the formulæ for the different varieties of sugar in a crystalline form:

Cane-Sugar, $C_{12}H_{11}O_{11}$
Milk-Sugar, $C_{12}H_{12}O_{12}$
Grape-Sugar (*Glucose*), $C_{12}H_{14}O_{14}$

All varieties of sugar have a peculiar sweet taste; they are soluble in water and in alcohol; they are inflammable, leaving an abundant carbonaceous residue and giving off a peculiar odor of caramel; they are capable of being converted, in contact with ferments or with nitrogenized principles, into alcohol and carbonic acid and into lactic acid; they are also capable of other modifications when treated with the mineral acids, or with alkalies, which are interesting more in a chemical than a physiological point of view. Of all the varieties of sugar, that made from the sugar-cane is the most soluble,

[1] The name hydro-carbon is strictly applicable only to the sugars and starch, which are, chemically, hydrates of carbon, containing as they do, carbon, with hydrogen and oxygen in the proportions to form water.

the sweetest, and the most agreeable. Beet-root sugar, so extensively used in France, is perhaps as agreeable, but is not so sweet.

Much of the sugar used in the nutrition of the organism is formed in the body from the digestion of starch. This transformation of starch may be effected artificially. The sugar thus formed is called glucose and is identical in composition with grape-sugar. Except in the milk during lactation, this is the only form in which sugar exists in the organism, all the sugar of the food being converted into glucose before it is taken into the blood.

Starch.—A non-nitrogenized principle, closely resembling sugar in its ultimate composition ($C_{12}\, H_{10}\, O_{10}$), is contained in abundance in a great number of vegetables. It is found particularly in the cereals (wheat, rye, corn, barley, rice, and oats), in the potato, chestnuts, and in the grains of leguminous plants (beans, peas, lentils, and kidney-beans), in the tuberous roots of the yam, tapioca, and sweet-potato, in the roots of the *Maranta arundinacea*,[1] in the sago-plant, and in the bulbs of orchis. In the cereals, after desiccation, the proportion of starch is, in general terms, between sixty and seventy parts per hundred. It is most abundant in rice, which contains, after desiccation, 88·65 parts per 100.

Starch may be separated from many plants by simple washing, but in others, in which it exists in connection with a considerable proportion of gluten, a more elaborate process is employed in commerce. The different varieties of manufactured starch, such as corn-starch, potato-starch, arrow-root, tapioca, and sago, differ only in the presence of a minute quantity of odorous and flavoring principles.

When extracted in a pure state, starch is in the form of granules, varying in size from $\frac{1}{10000}$ to $\frac{1}{400}$ of an inch, and presenting, in most varieties, certain peculiarities of form. The granule is frequently marked by a little conical excavation called the hilum, and the starch-substance is arranged in the form of concentric laminæ, the outlines of which are frequently quite distinct. When starch is rubbed between the fingers, these little hard bodies give it rather a gritty feel and produce a crackling sound. The different varieties of starch may be recognized microscopically by the peculiar appearance of the granules.

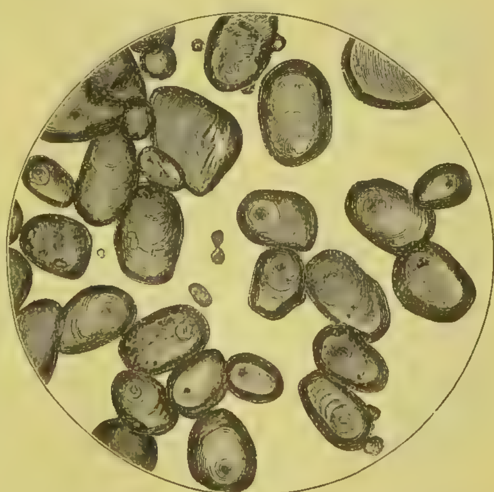


Fig. 44.—*Arrow-root starch-granules; magnified* 370 *diameters.* (From a photograph taken at the United States Army Medical Museum.)

The presence of even a minute quantity of starch in any mixture which is not alkaline may be readily determined by the addition of iodine, which unites with the starch, producing an intense-blue color. The color may be destroyed by the addition of an alkali or by the application of heat. It may be restored, however, by the addition of an acid or, in the latter instance, it returns when the mixture is allowed to cool, if the temperature have not been carried to 212° Fahr.

Starch is insoluble in water, but, when boiled with several times its volume of water, the granules swell up, become transparent, and finally fuse together, mingling with the water and giving it a mucilaginous consistence. The mixture on cooling forms a jelly-like mass of greater or less consistence. This change in starch is called hydration and is interesting as one of the transformations which takes place in the process of digestion,

[1] The creeping roots from which the substance known as arrow-root is manufactured.

when starch is taken uncooked. This change is generally effected, however, in the process of cooking.

The most interesting properties of starch are connected with its transformation, first into dextrine and finally into glucose. This always takes place in digestion, before starch can be absorbed. In the digestive apparatus, the change into sugar is almost instantaneous, and the intermediate substance, dextrine, is not recognized. By boiling starch for a number of hours with dilute sulphuric acid, it gradually loses its property of striking a blue color with iodine, and is transformed, without any change in chemical composition, into the soluble substance called dextrine. If the action be continued, it assumes four atoms of water and is converted into glucose. If dextrine be perfectly pure, no coloration is produced by the addition of iodine, but it ordinarily contains starch imperfectly transformed, and iodine produces a reddish color. The change of starch into dextrine may be effected by a dry heat of about 400° Fahr., a process which is commonly employed in commerce. The most effectual method of producing this transformation of starch, aside from the process of digestion, is by the action of a peculiar vegetable substance called diastase. This substance is produced in the process of germination of many of the vegetables containing starch.[1] One part of diastase will effect the transformation of one hundred parts of starch, which would require thirty times the quantity of sulphuric acid. What has been said regarding sugar as an alimentary principle will apply to starch. Although an abundant and important article of diet, it is insufficient of itself for the purposes of nutrition.

Vegetable Principles resembling Starch.—In certain vegetables, substances isomeric with starch, but presenting slight differences as regards general properties and reactions, have been described, but they possess no very great interest as alimentary principles and demand only a passing mention. These are, inuline, lichenine, cellulose, pectose, mannite, mucilages, and gums. Inuline is found in certain roots. It is capable of being converted into sugar but does not pass through the intermediate stage of dextrine. It differs from starch in being very soluble in hot water and in striking a yellow instead of a blue color with iodine. Lichenine is found in many kinds of edible mosses and lichens. It differs from starch only in its solubility.

Cellulose is a substance, generally regarded as identical in all plants, which forms the basis of the walls of the vegetable cells. It exists in greater or less abundance in all vegetables. It is less easily acted upon by acids than starch, but is capable, when treated with concentrated sulphuric acid, of being converted first into dextrine, and finally into sugar. It is only in soft and recent vegetable products that it can be regarded as an alimentary principle.

Pectose is a principle which exists, mingled with cellulose, in unripe fruits, carrots, turnips, and some other vegetables of this class. Its composition has not been determined. In ripe fruits, it is found transformed into a soluble substance called pectine. This transformation may be effected artificially by the action of acids and heat. Pectine may be precipitated in a gelatinous form by alcohol from the juices of fruits.

Mannite is a sweetish principle found in manna, mushrooms, celery, onions, and asparagus. Manna in tears is composed of this principle in nearly a pure state. It is perhaps more analogous to sugar than to starch, but it is not capable of fermentation and has no influence on polarized light.

Gums and mucilages may enter to a certain extent into the composition of food, but they can hardly be considered as alimentary principles. Gums are found exuding from certain trees, first in a fluid state, but becoming hard on exposure to the air. A viscid, stringy mucilage is found surrounding many grains, such as the flax-seed and quince-seeds, and exists in various kinds of roots and leaves. Both gums and mucilages mix readily

[1] Diastase is a white, amorphous, nitrogenized substance, insoluble in alcohol, soluble in water, and is extracted from barley, oats, grain, and potatoes, in process of germination. Its action upon starch is most energetic at from 150° to 167° Fahr.

with water, giving it a consistence called mucilaginous. They have the same composition as starch.

Experiments have shown that gum passes through the alimentary canal unchanged and has no nutritive power. It is said that gummy exudations from trees form an important part of the food of certain savage African tribes; but it must be remembered that in this condition the exudation is impure and contains many other substances. Gum is mentioned in this connection from the fact that it is frequently used in the treatment of disease and is thought by many to possess nutritive properties.

Fats and Oils.—Fatty or oily matters, derived from both the animal and the vegetable kingdom, constitute an important division of the articles of food. As a proximate principle, fat is found in all parts of the body, with the exception of the bones, teeth, and fibrous tissues. It necessarily constitutes an important part of all animal food and is taken in the form of adipose tissue, infiltrated in the various tissues in the form of globules and granules of oil, and in suspension in the caseine and water in milk. Animal fat is a mixture of oleine, margarine, and stearine, in varied proportions, and possesses a consistence which depends upon the relative quantities of these principles. More or less fat always enters into the composition of food, but, as a rule, it is more abundantly taken in cold than in warm climates. The ordinary diet of the Greenlander contains what would be considered in temperate climates as an enormous quantity of fat and oil, frequently in a disgusting form, and often taken unmixed with other articles.

The different varieties of animal fats do not demand special consideration as articles of diet. Butter, an important article of food, is somewhat different from the fat extracted from adipose tissue, but most varieties of fat lose their individual peculiarities in the process of digestion and are apparently identical when they find their way into the lacteal vessels.

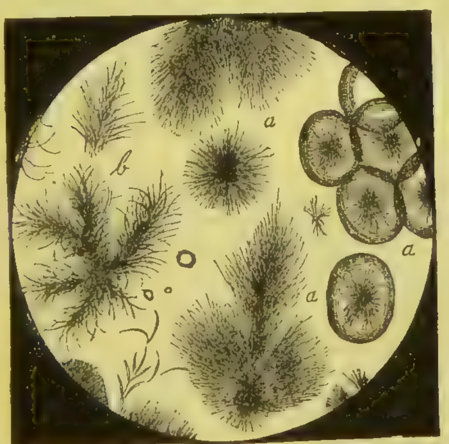


FIG. 45.—*Crystals of margarine and margaric acid.* (Funke.) *a, a, a,* margarine; *b,* margaric acid.

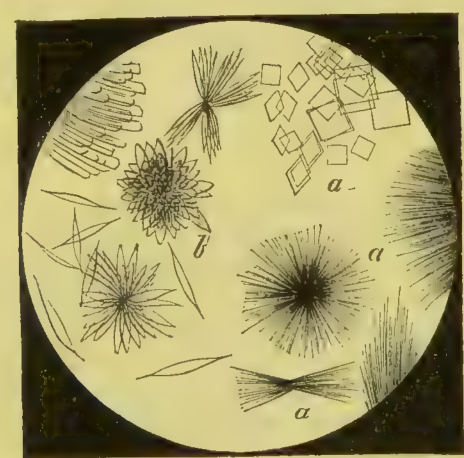


FIG. 46.—*Crystals of stearine and stearic acid.* (Funke.) *a, a, a,* stearine; *b,* stearic acid.

In the vegetable kingdom, fat is particularly abundant in seeds and grains, but it exists in quantity in some fruits, as the olive. Here it is generally called oil. Its proportion in linseed is 20 per cent.; in rape-seed, 35 to 40 per cent.; in hemp-seed, 25 per cent.; and in poppy-seed, 47 to 50 per cent. It exists in considerable proportion in nuts and in certain quantity in the cereals, particularly Indian corn. Its proportion in the different varieties of wheat is from 1·87 to 2·61 per cent.; in rye, 2·25 per cent.; in barley, 2·76 per cent.; in oats, 5·5 per cent.; in Indian corn, 8·8 per cent.; and in rice, 0·8 per cent. The above is the proportion in the grains after desiccation.

Fat, both animal and vegetable, may be either liquid or solid. It has a peculiar oily feel, a neutral reaction, and is insoluble in water and soluble in alcohol (particularly hot alcohol), chloroform, ether, benzine, and solutions of soaps. The solid varieties are exceedingly soluble in the oils. Treated with alkalies, at a high temperature and in the presence of water, the fats are decomposed into fatty acids and glycerine, the acid uniting with the base to form a soap. Alkaline, mucilaginous, and some animal fluids (particularly the pancreatic juice) are capable of holding fat in a state of minute and permanent subdivision and suspension, forming what are known as emulsions.

The composition of many of the fats and oils has never been definitely ascertained, on account of the difficulty in obtaining them in a state of absolute purity. They contain carbon, hydrogen, and oxygen, but the latter elements do not exist in the proportions to form water.

As alimentary principles, fats and oils are undoubtedly of great importance. They are supposed by many to be particularly concerned in the function of calorification. It has been proven by repeated experiments that fat, as a single article of diet, is insufficient for the purposes of nutrition.

Inorganic Alimentary Principles.

Physiological chemistry has shown that all the organs, tissues, and fluids of the body contain inorganic matter in greater or less abundance. The same is true of vegetable products. All the organic nitrogenized principles contain mineral substances which cannot be removed without incineration and which must be considered as actually part of their substance. When new organic matter is appropriated by the tissues to supply the place of that which has become effete, the mineral substances are deposited with them; and the organic principles, as they become effete or are transformed into excrementitious substances and discharged from the body, are always thrown off in connection with the mineral substances which enter into their composition. This constant discharge of inorganic principles, forming, as they do, an essential part of the organism, necessitates their introduction with the food, in order to maintain the normal constitution of the parts. As these principles are as necessary to the proper constitution of the body as any other, they must be considered as belonging to the class of alimentary substances.

Water.—This is one of the most important of the proximate principles of the organism, is found in every tissue and part without exception, is introduced with all kinds of food, and is the basis of all drinks. As a rule, it is taken in greater or less quantity in a nearly pure state. Although, as a drink, water should be colorless, odorless, and nearly tasteless, it always contains more or less saline and other matters in solution, with a certain quantity of air. The air and gases may be evolved by boiling or removing the atmospheric pressure. Pure water does not exist in Nature. Even rain-water always contains salts and frequently a little ammonia and organic matter. The waters of the mineral springs, which are so abundant in parts of this country, are very rich in saline constituents and generally contain a notable quantity of carbonic acid; but the consideration of their properties does not belong to physiology. The demand on the part of the system for water is regulated, to a certain extent, by the quantity discharged from the organism, and this is subject to great variations. The quantity taken as drink also depends very much on the constitution of the food as regards the water which enters into its composition.

Chloride of Sodium.—Of all saline substances, chloride of sodium is the one most widely distributed in the animal and the vegetable kingdom. It exists in all varieties of food; but the quantity which is taken in combination with other principles is usually insufficient for the purposes of the economy, and common salt is generally added to certain articles of food as a condiment, when it improves their flavor, promotes the secretion of certain of the digestive fluids, and meets a positive nutritive demand on the part of the system. Numerous experiments and observations have shown that a deficiency of chloride of sodium in the food has an unfavorable influence on nutrition.

Phosphate of Lime.—This is almost as common a constituent of vegetable and animal food as chloride of sodium. It is seldom taken except in combination, particularly with the nitrogenized alimentary principles. Its importance as an alimentary principle has been experimentally demonstrated, it having been shown that, in animals deprived as completely as possible of this substance, the nutrition of the body, particularly in parts which contain it in considerable quantity, as the bones, is seriously affected.

Iron.—Hæmaglobine, the coloring matter of the blood, contains, intimately united with organic matter, a considerable proportion of iron. Examples of anæmia, which are daily met with in practice and are almost always relieved in a short time by the administration of iron, are proof of the importance of this substance as an alimentary principle. The quantity of iron which is discharged from the body is very slight, a trace only being discoverable in the urine. A small quantity of iron is frequently introduced in solution in the water taken as drink, and it is a constant constituent of milk and eggs. When its supply in the food is insufficient, it is necessary, in order to restore the processes of nutrition to their normal condition, to administer it in some form, until its proportion in the organism reaches the proper standard.

It is hardly necessary even to enumerate the other inorganic alimentary principles, as nearly all are in a state of such intimate combination with nitrogenized principles that they may be regarded as part of their substance. Suffice it to say, that all the inorganic matters which exist in the organism as proximate principles are found in the food. That these are essential to nutrition, cannot be doubted; but it is evident that, by themselves, they are incapable of supporting life, as they cannot be converted into either nitrogenized or non-nitrogenized organic principles.

Alcohol.

All distilled and fermented liquors and wines contain a greater or less proportion of alcohol. As these are so generally used as beverages, and as the effects of their excessive use are so serious, the influence of alcohol upon the organism has become one of the most important questions connected with alimentation. In the discussion of this subject, it is not proposed to enter into the great moral questions involved, but to consider, from a purely physiological point of view, the immediate and remote influences of the various alcoholic beverages upon nutrition and the animal functions. Some alcoholic beverages influence the functions solely through the alcohol which they contain; while others, as beer and porter, with a comparatively small proportion of alcohol, contain a considerable quantity of solid matters which may act as alimentary principles.

Alcohol ($C_4H_6O_2$), from its composition, is to be classed with the non-nitrogenized principles, more especially the fats, in which the hydrogen and oxygen do not exist in the proportion to form water. We have seen that sugar and fat are essential to proper nutrition and that they undergo important changes in the organism. Alcohol is capable of being absorbed and taken into the blood; and it becomes a question of great interest to determine whether it be consumed in the economy or whether it be discharged unchanged by the various emunctories.

Alcohol has long since been recognized in the expired air after it has been taken into the stomach; and late researches have confirmed the earlier observations with regard to its elimination in its original form and have shown that, after it has been taken in quantity, it exists in the blood and all the tissues and organs, particularly the liver and nervous system.[1] Lallemand, Perrin, and Duroy have stated, also, that there is a considerable elimination of alcohol by the lungs, skin, and kidneys; but the accuracy of the experiments by which these results were arrived at has lately been questioned. The recent observations of Drs. Anstie and Dupré have, indeed, thrown great doubt upon the chromic-acid test for alcohol, which was employed by the French observers above mentioned. Anstie and Dupré have clearly shown that the color-test applied to the urine of persons who do not drink alcohol at all not only acts with chromic acid in the same way as does alcohol, but that the substance in the urine, whatever it may be, "is capable of being similarly oxidized into an acid which is apparently identical with acetic acid, and similarly converted to iodoform by boiling with iodine and an alkali." Nevertheless, when alcohol has been taken in narcotic doses, there is a certain amount of alcoholic elimination in the urine, as was shown long ago by Percy. We are not, however, considering at present the elimination of alcohol when the ingestion of this principle has been pushed to extreme intoxication, but only the question whether moderate doses of alcohol be eliminated in totality or be consumed in the organism in the same way as sugar or albumen. It is possible to administer, for example, such quantities of sugar that a certain amount will pass off in the urine; and no one supposes that moderate quantities of sugar are not consumed in the organism. As the result of the final experiments of Anstie, it is absolutely certain that most of the alcohol which is taken in quantities not sufficient to produce alcoholic intoxication is consumed in the organism, and but a trivial amount is thrown off, either in the urine, the fæces, the breath, or the cutaneous transpiration. This question is of the greatest importance with regard to the moderate use of alcohol under normal conditions, and especially in its bearing upon the therapeutical action of the various alcoholic drinks administered in cases of disease.

Taken in moderate quantity, alcohol generally produces a certain amount of nervous exaltation, which gradually passes off. In some individuals the mental faculties are sharpened by alcohol, while in others they are blunted. There is nothing, indeed, more variable than the immediate effects of alcohol on different persons. In large doses, the effects are the well-known phenomena of intoxication, delirium, more or less anæsthesia, coma, and sometimes, if the quantity be excessive, death. As the rule, the mental exaltation produced by alcohol is followed by reaction and depression, except in debilitated or exhausted conditions of the system, when the alcohol seems to supply a decided want.

The views of physiologists concerning the influence of a moderate quantity of alcohol on the nervous system are somewhat conflicting. That it may temporarily give tone and vigor to the system when the energies are unusually taxed, cannot be doubted; but this effect is not produced in all individuals. The constant use of alcohol may create an apparent necessity for it, producing a condition of the system which must be regarded as pathological.

The immediate effects of the ingestion of a moderate quantity of alcohol, continued for a few days, are decided. It notably diminishes the exhalation of carbonic acid and the discharge of other excrementitious principles, particularly urea. These facts have long since been experimentally demonstrated. The proper amount of mental and physical exercise, tranquillity of the nervous system, and all circumstances which favor the vigorous nutrition and development of the organism physiologically increase, rather than diminish, the amount of the excretions, correspondingly increase the demand for food, and, if continued, are of permanent benefit. Alcohol, on the other hand, diminishes the activity of nutrition. If its use be long continued, the assimilative powers of the system

[1] It was formerly a question considerably discussed whether alcohol exist in the brain and in the fluid found in the ventricles, in intoxicated persons. This was settled by Percy, who found alcohol in the brain, liver, and sometimes in the urine, in dogs poisoned with alcohol and in men who had died after excessive drinking. In these experiments, the presence of alcohol was determined by distillation, the distilled substances being inflammable and capable of dissolving camphor.—PERCY, *Prize Thesis. An Experimental Inquiry concerning the Presence of Alcohol in the Ventricles of the Brain, etc.*, London, 1839.

become so weakened that the proper quantity of food cannot be appropriated, and alcohol is craved to supply a self-engendered want. The organism may, in many instances, be restored to its physiological condition by discontinuing the use of alcohol; but it is generally some time before the nutritive powers become active, and alcohol, meanwhile, seems absolutely necessary to existence.

Under ordinary conditions, when the organism can be adequately supplied with food, alcohol is undoubtedly injurious. When the quantity of food is insufficient, alcohol may supply the want for a time and temporarily restore the powers of the body; but the effects of its continued use, conjoined with insufficient nourishment, show that it cannot take the place of assimilable matter. These effects are too well known to the physician, particularly in hospital-practice, to need farther comment. Notwithstanding these undoubted physiological facts, alcohol, in some form, is used by almost every people on the face of the earth, civilized or savage. Whether this be in order to meet some want occasionally felt by and peculiar to the human organism, is a question upon which physiologists have found it impossible to agree. That alcohol, at certain times, taken in moderation, soothes and tranquillizes the nervous system and relieves exhaustion dependent upon unusually severe mental or physical exertion, cannot be doubted. It is by far too material a view to take of existence, to suppose that the highest condition of man is that in which the functions, possessed in common with the lower animals, are most perfectly performed. Inasmuch as temporary insufficiency of food, great exhaustion of the nervous system, and various conditions in which alcohol seems to be useful, must of necessity often occur, it is hardly proper that this agent should be utterly condemned; but it is the article, *par excellence*, which is liable to abuse, and the effects of which on the mind and body, when taken constantly in excess, are most serious.

Although alcohol imparts a genial warmth when the system is suffering from excessive cold, it is not proven that it enables men to endure a very low temperature for a great length of time. This end can be effectually accomplished only by an increased quantity of food. The testimony of Dr. Hayes, the Arctic explorer, is very strong upon this point. He says: "While fresh animal food, and especially fat, is absolutely essential to the inhabitants and travellers in Arctic countries, alcohol is, in almost any shape, not only completely useless but positively injurious. . . . Circumstances may occur under which its administration seems necessary; such, for instance, as great prostration from long-continued exposure and exertion, or from getting wet; but then it should be avoided, if possible, for the succeeding reaction is always to be dreaded; and, if a place of safety is not near at hand, the immediate danger is only temporarily guarded against, and becomes, finally, greatly augmented by reason of decreased vitality. If given at all, it should be in very small quantities frequently repeated, and continued until a place of safety is reached. I have known the most unpleasant consequences to result from the injudicious use of whiskey for the purpose of temporary stimulation, and have also known strong able-bodied men to have become utterly incapable of resisting cold in consequence of the long-continued use of alcoholic drinks."

It is not demonstrated that alcohol increases the capacity to endure severe and protracted bodily exertion. Its influence as a therapeutic agent, in promoting assimilation in certain conditions of defective nutrition, in relieving shock and nervous exhaustion, in sustaining the powers of life in acute diseases characterized by rapid emaciation and abnormally active disassimilation, etc., is undoubted; but the consideration of these questions does not belong to physiology.

Coffee.

Coffee is an article consumed daily by many millions of human beings in all quarters of the globe. In armies it has been found almost indispensable, enabling men on moderate rations to perform an amount of labor which would otherwise be impossible. After exhausting efforts of any kind, there is no article which relieves the overpowering sense of fatigue so completely as coffee. Army-surgeons say that at night, after a severe march, the first desire of the soldier is for coffee, hot or cold, with or without sugar, the only essential being a sufficient quantity of the pure article. This has been the universal experience in the late civil war; the rations of coffee issued by the United States Government being abundant and pure, though not, of course, of the quality possessing the most delicate flavor. Almost every one can bear testimony from personal experience to the effects of coffee in relieving the sense of fatigue after mental or bodily exertion and in increasing the capacity for labor, especially mental, by producing wakefulness and clearness of intellect. From these facts, the importance of coffee, either as an alimentary article or as taking the place, to a certain extent, of aliment, is apparent.

Except in persons who, from idiosyncrasy, are unpleasantly affected by it, coffee, taken in moderate quantity and at proper times, produces an agreeable sense of tranquillity and comfort, with, however, no disinclination to exertion, either mental or physical. Its immediate influence upon the system, which is undoubtedly stimulant, is peculiar and is not followed by reaction or unpleasant after-effects. Habitual use renders coffee almost a necessity, even in those who are otherwise well nourished and subjected to no extraordinary mental or bodily strain. Taken in excessive quantity, or in those unaccustomed to its use, particularly when taken at night, it produces persistent wakefulness. These effects are so well known that it is often taken for the purpose of preventing sleep.

Experimental researches have shown that the use of coffee permits a reduction in the quantity of food, in workingmen especially, much below the standard which would otherwise be necessary to maintain the organism in proper condition. In the observations of De Gasparin upon the regimen of the Belgian miners, it was found that the addition of a quantity of coffee to the daily ration enabled them to perform their arduous labors on a diet which was even below that found necessary in prisons and elsewhere where this article was not employed. Numerous experiments have shown that coffee diminishes the absolute quantity of urea discharged by the kidneys. In this respect, as far as has been ascertained, the action of coffee is like that of alcohol and may reasonably be supposed to retard disassimilation, with the important difference that it is followed by no unfavorable after-effects and can be used in moderation for an indefinite time with advantage.

A study of the composition of coffee shows a considerable proportion of what must be considered as alimentary matter. The following is the result of the analyses of Payen:

Composition of Coffee.

Cellulose	34·000
Water (hygroscopic)	12·000
Fatty substances	10 to 13·000
Glucose, dextrine, indeterminate vegetable acid	15·500
Legumine, caseine, etc.	10·000
Chlorolignate of potash, and caffeine	3·5 to 5·000
Nitrogenized organic matter	3·000
Free caffeine	0·800
Concrete, insoluble essential oil	0·001
Aromatic essence, of agreeable odor, soluble in water	0·002
Mineral substances; potash, magnesia, lime, phosphoric, silicic, and sulphuric acid and chlorine	6·697
	100·000

The above is the composition of raw coffee, but the berry is seldom used in that form, being usually subjected to torrification before an infusion is made. The roasting should be conducted slowly and gently, until the grains assume a chestnut-brown color. During this process, the grains are considerably swollen, but they lose from sixteen to seventeen per cent. in weight. A peculiar aromatic principle is also developed by roasting. If the torrification be pushed too far, much of the agreeable flavor is lost, and an acrid empyreumatic principle is produced. An infusion of fifteen hundred grains of roasted and ground coffee in about a quart of boiling water, the infusion made by simple percolation, contains about three hundred grains of the soluble principles. According to Payen, this contains about one hundred and forty grains of nitrogenized matters and one hundred and fifty-three grains of fatty, saccharine, and saline substances. There is every reason to suppose that that these principles are assimilated; and an infusion of coffee, with milk and sugar, presents, therefore, a considerable variety and quantity of alimentary matter. The peculiar stimulant effects of coffee are probably due to the caffeine and volatile oil.

In the countries where coffee is grown, the leaves of the shrub, roasted and made into an infusion, are quite commonly used. Their effects upon the system are similar to those of coffee, and it is said that the natives prefer the leaves to the berry.

Tea.

An infusion of the dried and prepared leaves of the tea-plant is perhaps as common a beverage as coffee, and, taking into consideration its immense consumption in China and Japan, it is actually used by a greater number of persons. Its effects upon the system are similar to those of coffee, but are generally not so marked. Ordinary tea, taken in moderate quantity, like coffee, relieves fatigue and increases mental activity, but does not usually induce such persistent wakefulness.

It is unnecessary to describe all the varieties of tea in common use. There are, however, certain varieties, called green teas, which present important differences, as regards composition and physiological effects, from the black teas, which are more commonly used. The following is a comparative analysis of these two varieties by Mulder:

Composition of Tea.

Constituents.	Chinese.		Javanese.	
	Hyson.	Congou.	Hyson.	Congou.
Volatile oil	0·79	0·60	0·98	0·65
Chlorophylle	2·22	1·84	3·24	1·28
Wax	0·28	——	0·32	——
Resin	2·22	3·64	1·64	2·44
Gum	8·56	7·28	12·20	11·08
Tannin	17·80	12·88	17·56	14·80
Theine	0·43	0·46	0·60	0·65
Extractive	22·80	19·88	21·68	18·64
Apotheme	——	1·48	——	1·64
Extract obtained by hydrochloric acid	23·60	19·12	20·36	18·24
Albumen	3·00	2·80	3·64	1·28
Fibrous matter	17·08	28·32	18·20	27·00
	98·78	98·30	100·42	97·70
Salts included in the above	5·56	5·24	4·76	5·36

Both tea and coffee possess peculiar organic principles. The active principle of tea is called theine, and the active principle of coffee, caffeine. As they are supposed to be particularly active in producing the peculiar effects upon the nervous system which are characteristic of both tea and coffee, there is good reason to suppose that they are nearly identical in their physiological effects. Theine (or caffeine) exists in greater proportion in tea than in coffee; but, as a rule, much more soluble matter is employed in the preparation of coffee, which may account for its more marked effects upon the system.

Green tea, especially in those unaccustomed to its use, frequently produces nervous tremor, wakefulness, and disturbed sleep—when sleep can be obtained—palpitations, and other disturbances usually termed nervous. In some persons these unpleasant effects may be overcome by habit; and many constantly use a mixture of equal parts of black and green tea with no unpleasant effects. The peculiar effects of green tea are attributed to the volatile oil, which it contains in great abundance.

Tea is prepared for drinking by rapidly making an infusion of the leaves with hot water. The aroma is impaired by boiling. The proportion generally used is about three hundred grains of tea to a quart of water. The tea is first covered with boiling water and allowed to steep, or "draw," for from ten to fifteen minutes, in a warm place; boiling water is then added in the quantity desired. Green tea, treated in this way, yields about twenty per cent. of soluble matters, and black tea, about twenty-three per cent.

Chocolate.

Chocolate is made from the seeds of the cocoa-tree, roasted, deprived of their husks, and ground with warm rollers into a pasty mass with sugar, flavoring substances being sometimes added. It is then made into cakes, cut into small pieces or scraped to a powder, and boiled with milk or milk and water, when it forms a thick, gruel-like drink, which is highly nutritive and has some of the exhilarating properties of coffee or tea. Beside containing a large proportion of nitrogenized matter resembling albumen, the cocoa-seed is particularly rich in fatty matter and contains a peculiar principle, theobromine, analogous to caffeine and theine, which is supposed to possess similar physiological properties.

The following is an analysis by Payen of the cocoa-seeds freed from the husks but not roasted. Torrification has the effect of developing the peculiar aromatic principle, and moderating the bitterness, which is always more or less marked:

Composition of Kernels of Cocoa.

Fatty matter (cocoa-butter)	48 to 50
Albumen, fibrin, and other nitrogenized matter	21 " 20
Theobromine	4 " 2
Starch (with traces of saccharine matter)	11 " 10
Cellulose	3 " 2
Coloring matter, aromatic essence	traces.
Mineral substances	3 to 4
Hygroscopic water	10 " 12
	100 100

It is evident, from the above table, that cocoa with milk and sugar, the ordinary form in which chocolate is taken, must form a very nutritious mixture. Taken with a little bread, it readily relieves hunger and supplies nearly all the principles absolutely necessary to nutrition. Its influence as a stimulant, supplying the place of matter which is directly assimilated and retarding disassimilation, is dependent, if it exist at all, upon the theobromine; but its stimulating properties are slight as compared with those of coffee and tea.

A drink called cocoa is sometimes made of the seeds roasted entire and mixed with a little starchy matter, but this is not so delicate in flavor as chocolate. A brown, mucilaginous infusion is sometimes made of the husks (shells). This has a slight chocolate-flavor, but it does not possess the nutrient properties of the kernels of cocoa.

Condiments and Flavoring Articles.

The refinements of modern cookery involve the use of numerous articles which cannot be classed as alimentary principles. Pepper, capsicum, vinegar, mustard, spices, and articles of this class, which are so commonly used, with the various compound sauces, have no decided influence on nutrition, except in so far as they promote the secretion of the digestive fluids. Common salt, however, as we have already seen, is very important, and this has been considered under the head of inorganic alimentary principles. The various flavoring seeds and leaves, truffles, mushrooms, etc., have no physiological importance except as they render articles of food more palatable.

Quantity and Variety of Food necessary to Nutrition.

The inferior animals, especially those not subjected to the influence of man, regulate by instinct the quantity and kind of food which they consume. The same is true of man during the earliest periods of his existence; but, later in life, the diet is variously modified by taste, habit, climate, and what may be termed artificial wants. It is usually a safe rule to follow the appetite with regard to quantity, and the tastes, when they are not manifestly vitiated or morbid, with regard to variety. The cravings of Nature indicate when to change the form in which nutriment is taken; and that a sufficient quantity has been taken is manifested by a sense, not exactly of satiety, but of evident satisfaction of the demands of the system. During the first periods of life, the supply must be a little in excess of the actual loss, in order to furnish materials for growth; during the later periods, the quantity of nitrogenized matter assimilated is somewhat less than the loss; but, in adult age, the system is maintained at a tolerably definite standard by the assimilation of material about equal in quantity to that which is discharged in the form of excretions.

Although the loss of substance by disassimilation creates and regulates the demand for food, it is an important fact, never to be lost sight of, that the supply of food has a very great influence upon the quantity of the excretions. As an illustration of this, we may take the influence of food upon the exhalation of carbonic acid; and this is but an example of what takes place with regard to other excretions. The quantity of the excretions is even more strikingly modified by exercise, which, within physiological limits, increases the vigor of the system, provided the increased quantity of food required be supplied.

While a certain amount of waste of the system is inevitable, it is a conservative provision of Nature, that, when the supply of new material is diminished, life is preserved—not, indeed, in all its vigor—by a corresponding reduction in the quantity of excretions; and, in the same way, the forces are retained after complete deprivation of food much longer than if disassimilation proceeded always with the same activity.

As regards the quantity of food necessary to maintain the system in proper condition, it is evident that this must be greatly modified by habit, climate, the condition of the muscular system, age, sex, etc., as well as idiosyncrasies.

The daily loss of substance which must be supplied by material introduced from without is very great. A large portion of this discharge takes place by the lungs, and a consideration of the mode of introduction of gaseous principles to supply part of this waste belongs to the subject of respiration. The most abundant discharge which is compensated by absorption from the alimentary canal is that of water, both in a liquid and vaporous condition. The entire quantity of water daily removed from the system has been estimated at about four and a half pounds; and, assuming that there is no evidence of the production of water in the organism, an equal quantity must necessarily be introduced. The quantity which is taken in the form of drink varies with the character of the food. When the solid articles contain a large proportion of water, the quantity of drink may be diminished; and it is possible, by taking a large proportion of the watery vegetables, to exist entirely without drink. There is no article the consumption of which is so much a matter of habit as water, any excess which may be taken being readily removed by the kidneys, skin, and lungs. Prof. Dalton estimates the daily quantity necessary for a full-grown, healthy male, at fifty-two fluid ounces, or 3·38 lbs. avoirdupois.

The quantity of solid food necessary to the proper nourishment of the body is shown by estimating the solid matter in the excretions; and the facts thus ascertained correspond very closely with the quantity of material which the system has been found to actually demand. The estimates of Payen, the quantity of carbon and of nitrogenized matter in a dry state being given, are generally quoted and adopted in works on physiology. According to this observer, the following are the daily losses of the organism:

Carbon (or its equivalent)....	Respiration, 3,868·5 grs. Excretions, 926·04 "	4,794·54 grs. (10·93 oz. av.)
Nitrogenized substances......	(with 308·68 grs. of nit.)	2,006·42 grs. (4·58 oz. av.)
		6,800·96 grs. (15·51 oz. av.)

From this he estimates that the normal ration, supposing the food to consist of lean meat and bread, is as follows:

		Nitrogenized substances.		Carbon.
Bread.............	15,434 grs. (35·27 oz.) =	1,080·38 grs.	and	4,630·2 grs.
Meat..............	4,412·12 grs. (10·09 oz.) =	930·05 grs.	and	485·55 grs.
	19,846·12 grs. (45·36 oz.)	2,010·43 grs.		5,115·75 grs.

This daily ration, which is purely theoretical, is shown by actual observation to be nearly correct. Prof. Dalton says: "From experiments performed while living on an exclusive diet of bread, fresh meat, and butter, with coffee and water for drink, we have found that the entire quantity of food required during twenty-four hours by a man in full health and taking free exercise in the open air, is as follows:

Meat....................................	16 ounces, or	1·00 lb. avoirdupois.
Bread...................................	19 " "	1·19 " "
Butter or fat...........................	$3\frac{1}{2}$ " "	0·22 " "
Water...................................	52 fluid oz. "	3·38 " "

That is to say, rather less than two and a half pounds of solid food, and rather over three pints of liquid food."

Bearing in mind the great variations in the nutritive demands of the system in different persons, it may be stated, in general terms, that, in an adult male, from ten to twelve ounces of carbon and from four to five ounces of nitrogenized matter (estimated dry) are discharged from the organism and must be replaced by the ingesta; and this demands a daily consumption of from two to three pounds of solid food, the quantity of food depending, of course, greatly on its proportion of solid, nutritive principles.

It is undoubtedly true that the daily ration has frequently been diminished considerably below the physiological standard in charitable institutions, prisons, etc.; but, when there is complete inactivity of body and mind, this produces no other effect than that of slightly diminishing the weight and strength. The system then becomes reduced without any actual disease, and there is simply a diminished capacity for labor. But in the alimentation of large bodies of men subjected to exposure and frequently called upon to perform severe labor, the question of food is of vital importance, and the men collectively are like a powerful machine in which a certain quantity of material must be furnished in order to produce the required amount of force. This important physiological fact is most strikingly exemplified in armies; and the history of the world presents few examples of warlike operations in which the efficiency of the men has not been impaired by insufficient food.

The influence of diet upon the capacity for labor was well illustrated by a comparison of the amount of work accomplished by English and French laborers in 1841, on a railroad from Paris to Rouen. The French laborers engaged on this work were able at first to perform only about two-thirds of the labor accomplished by the English. It was suspected that this was due to the more substantial diet of the English, which proved to be the fact; for, when the French laborers were subjected to a similar regimen, they were able to accomplish an equal amount of work. In all observations of this kind, and they are very numerous, it has been shown that an animal diet is much more favorable to the development of the physical forces than one consisting mainly of vegetables.

Climate has an important influence on the quantity of food demanded by the system. It is generally acknowledged that the consumption of all kinds of food is greater in cold than in warm climates, and almost every one has experienced in his own person a considerable difference in the appetite at different seasons of the year. Travelers' accounts of the quantity of food taken by the natives of the frigid zone are almost incredible. They speak of men consuming over a hundred pounds of meat in a day; and a Russian admiral, Saritcheff, mentions an instance of a man who, in his presence, ate at a single meal a mess of boiled rice and butter weighing twenty-eight pounds. Although it is difficult to regard these statements with entire confidence, the general opinion that the appetite is greater in cold than in warm climates is undoubtedly well founded. Dr. Hayes, the Arctic explorer, states, from his personal observation, that the daily ration of the Esquimaux is from twelve to fifteen pounds of meat, about one-third of which is fat. On one occasion he saw an Esquimau consume ten pounds of walrus-flesh and blubber at a single meal, which lasted, however, several hours. The continued low temperature he found had a remarkable effect on the tastes of his own party. With the thermometer ranging from −60° to −70° Fahr., there was a continual craving for a strong animal diet, particularly fatty substances. Some members of the party were in the habit of drinking the contents of the oil-kettle with evident relish.

Necessity of a Varied Diet.

In considering the nutritive value of the various alimentary principles, the fact that no single one of them is capable of supplying all the material for the regeneration of the organism has frequently been mentioned. The normal appetite, which is our best guide as regards the quantity and the selection of food, indicates that a varied diet is necessary to proper nutrition. This fact is also exemplified in a marked degree in long voyages and in the alimentation of armies, when, from necessity or otherwise, the necessary variety of aliment is not presented. Analytical chemistry fails to show why this change in alimentary principles is necessary, or in what the deficiency in a single kind of diet consists; but it is nevertheless true that, after the organic constituents of the organism have appropriated the nutritious elements of particular kinds of food for a certain time, they lose the power of inducing the changes necessary to proper nutrition, and a supply of other material is imperatively demanded. This fact is particularly well marked when the diet consists in great part of salted meats, although it is also the case when any single variety of fresh meat is constantly used. After long confinement to a diet restricted as regards variety, a supply of other material, such as fresh vegetables, the organic acids, and articles which are called generally anti-scorbutics, becomes indispensable; otherwise, the modifications in nutrition and in the constitution of the blood incident to the scorbutic condition are almost sure to be developed.

It is thus apparent that adequate quantity and proper quality of food are not all that are required in alimentation; and those who have the responsibility of regulating the diet of a large number of persons must bear in mind the fact that the organism demands considerable variety. Fresh vegetables, fruits, etc., should be taken at the proper seasons. It is almost always found, when there is of necessity some sameness of diet, that there is a general craving for particular articles, and these, if possible, should be supplied. This was frequently exemplified in the late war. At times when the diet was necessarily somewhat monotonous, there was an almost universal craving for onions and raw potatoes, which were found by the surgeons to be excellent anti-scorbutics.

With those who supply their own food, the question of variety of diet generally regulates itself; and in institutions, it is a good rule to follow as far as possible the reasonable tastes of the inmates. In individuals, particularly females, it is not uncommon to observe marked disorders in nutrition attributable to want of variety in the diet as well as to an insufficient quantity of food, as a matter of education or habit.

The physiological effects of a diet restricted to a single alimentary principle or to a few articles have been pretty closely studied both in the human subject and in the inferior animals. Magendie demonstrated long ago that animals subjected to a diet composed exclusively of non-nitrogenized articles die in a short time with all the symptoms of inanition. The same result followed in dogs confined to white bread and water; but these animals lived very well on the military brown bread, as this contains a greater variety of alimentary principles. Facts of this nature were multiplied by the "gelatine commission," and the experiments were extended to nitrogenized substances and articles containing a considerable variety of alimentary principles. In these experiments, it was shown that dogs could not live on a diet of pure musculine, the appetite entirely failing, at from the forty-third to the fifty-fifth day. They were nourished perfectly well by gluten, which, as we have seen, is composed of a number of different alimentary principles. Among the conclusions arrived at by this commission, which bear particularly on the questions under consideration, were the following:

"Gelatine, albumen, fibrin, taken separately, do not nourish animals except for a very limited period and in a very incomplete manner. In general, these substances soon excite an insurmountable disgust, to the point that animals prefer to die of hunger rather than touch them.

"The same principles artificially combined and rendered agreeably sapid by seasoning are accepted more readily and longer than if they were isolated, but ultimately they have no better influence on nutrition, for animals that take them, even in considerable quantity, finally die with all the signs of complete inanition.

"Muscular flesh, in which gelatine, albumen, and fibrin are united according to the laws of organic nature, and when they are associated with other matters, such as fat, salts, etc., suffices, even in very small quantity, for complete and prolonged nutrition."

In Burdach's treatise on physiology, is an account of some interesting experiments by Ernest Burdach on rabbits, showing the influence of a restricted diet upon nutrition. Three young rabbits from the same litter were experimented upon. One was fed with potato alone and died on the thirteenth day with all the appearances of inanition. Another fed on barley alone died in the same way during the fourth week. The third was fed alternately day by day with potato and barley, for three weeks, and afterward with potato and barley given together. This one increased in size and was perfectly well nourished.

In 1769, long before any of the above-mentioned experiments were performed, Dr. Stark, a young English physiologist, fell a victim at an early age to ill-judged experiments on his own person on the physiological effects of different kinds of food. He lived for forty-four days on bread and water, for twenty-nine days on bread, sugar, and water, and for twenty-four days on bread, water, and olive-oil; until finally his constitution became broken, and he died from the effects of his experiments.

CHAPTER VII.

DIGESTION, MASTICATION, INSALIVATION, AND DEGLUTITION.

General arrangement of the digestive apparatus—Prehension of solids and liquids—Mastication—Physiological anatomy of the teeth—Anatomy of the maxillary bones—Temporo-maxillary articulation—Muscles of mastication—Muscles which depress the lower jaw—Action of the muscles which elevate the lower jaw and move it laterally and antero-posteriorly—Action of the tongue, lips, and cheeks in mastication—Summary of the process of mastication—Parotid saliva—Submaxillary saliva—Sublingual saliva—Fluids from the smaller glands of the mouth, tongue, and fauces—Mixed saliva—Quantity of saliva—General properties and composition of the saliva—Action of the saliva on starch—Mechanical functions of the saliva—Deglutition—Physiological anatomy of the parts concerned in deglutition—Muscles of the pharynx—Muscles of the soft palate—Mucous membrane of the pharynx—Œsophagus—Mechanism of deglutition—First period of deglutition—Second period of deglutition—Protection of the posterior nares during the second period of deglutition—Protection of the opening of the larynx—Function of the epiglottis—Study of deglutition by autolaryngoscopy—Third period of deglutition—Intermittent contraction of the lower third of the œsophagus—Nature of the movements of deglutition—Deglutition of air.

The inorganic alimentary principles are, with few exceptions, introduced in the form in which they exist in the blood and require no preparation or change before they are absorbed; but the organic nitrogenized principles are always united with more or less matter possessing no nutritive properties, from which they must be separated, and, even when pure, they always undergo certain changes before they become part of the great nutritive fluid. The non-nitrogenized principles also undergo changes in constitution or in form preparatory to absorption. With the varied forms in which food is taken by different animals, we find great differences in the arrangement of the digestive apparatus, from the simple pouch with a single orifice, which constitutes the entire digestive system of many of the infusorial animalcules, to the immense length of intestine, with its numerous glandular appendages, found in the mammalia. In the higher classes of animals, great differences exist in the anatomy of the digestive organs, particularly as regards the length and capacity of the alimentary canal. In the carnivora, in which the food contains comparatively little indigestible residue, the intestine is but three or four times the length of the body (*i. e.* from the mouth to the anus), and the colon, which receives the residue of digestion, is of small capacity; while in the herbivora, in which the bulk of food, compared with its nutritious principles, is enormous, there are frequently four distinct cavities to the stomach, and the intestine is ten, twelve, and in some (the sheep) twenty-eight times the length of the body, with a colon of very large size. The food of man is derived from both the animal and the vegetable kingdom, and, in relative length and capacity, the alimentary canal is between that of the carnivora and the herbivora, being from six to seven times the length of the body.

A full meal probably occupies from two to four hours in its digestion, this depending, of course, upon the kind of food, the fineness of its comminution by mastication, etc. The matters taken into the stomach consist generally of all varieties of alimentary principles, and they are exposed to certain mechanical processes in the mouth and alimentary canal and to the action of various secreted fluids.

In the mouth, the food is divided, as occasion demands, by the incisor teeth, and is then passed, by the action of the cheeks and tongue, between the molars, where it is subjected to mastication. During this process, it is mixed with the various fluids which compose the saliva and becomes more or less coated with the tenacious secretions of the mucous follicles of the buccal cavity. It is, or should be, reduced in the mouth to a pultaceous mass, with which the saliva, particularly that from the parotid gland, is thoroughly incorporated. The secretion of the submaxillary and the sublingual gland, being more viscid, has a tendency to coat the exterior of the alimentary bolus.

By the action of the tongue, the alimentary bolus, after mastication, is passed back to the pharynx, where, by the successive action of the constrictor muscles, it is forced into the œsophagus. This tube leads from the pharynx to the stomach and is provided with thick muscular walls, by the contraction of which the food is passed into this cavity, which serves at once as a receptacle for the food and an important active organ in digestion.

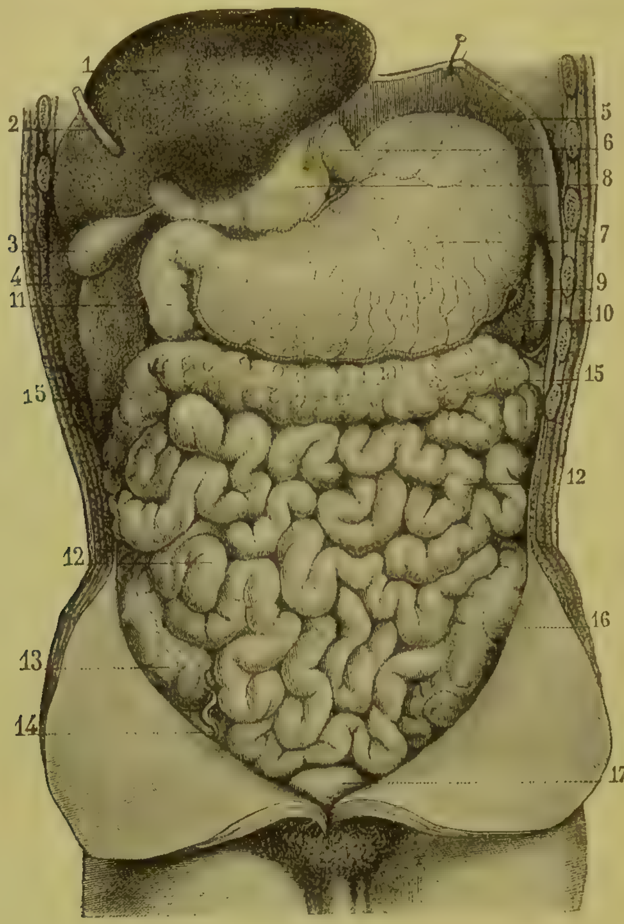


FIG. 47.—*Stomach, liver, small intestine, etc.* (Sappey.)

1, *inferior surface of the liver*; 2, *round ligament of the liver*; 3, *gall-bladder*; 4, *superior surface of the right lobe of the liver*; 5, diaphragm; 6, lower portion of the œsophagus; 7, *stomach*; 8, gastro-hepatic omentum; 9, spleen; 10, gastro-splenic omentum; 11, *duodenum*; 12, 12, *small intestine*; 13, *cæcum*; 14, *appendix vermiformis*; 15, 15, *transverse colon*; 16, *sigmoid flexure of the colon*; 17, urinary bladder.

The stomach is covered externally by the general peritoneal covering of the abdominal organs. It is provided with a mucous membrane, which secretes the gastric juice and absorbs the water with inorganic and other principles in solution. The stomach also has muscular walls, composed of unstriped muscular fibres arranged in two principal layers. Nearly all the principles contained in food are modified by the gastric juice, and some are completely liquefied and absorbed in the stomach. By the action of the gastric juice, the food, comminuted and incorporated with the fluids of the mouth, is farther reduced to a pultaceous mass, which was formerly called the chyme, the muscular movements of the stomach turning it over and over, so that it becomes thoroughly incorporated with the fluids. These movements have a tendency to force the food, as it becomes sufficiently liquefied, into the small intestine; and a collection of circular muscular fibres, called sometimes the pyloric muscle, stands at the pylorus as a guard, allowing the liquid portions to pass gradually through, but sending back the larger masses to be farther acted upon in the stomach. By these movements, a great portion of the food, prepared by the action of the stomach, is slowly forced into the small intestine. This tube, from fifteen to twenty feet in length, is covered with peritoneum and loosely bound to the spinal column by the mesentery, which is formed of the two folds of the peritoneum and is sufficiently long to allow of free movements of the intestines over each other and in the abdominal cavity, except the first few inches, where it is pretty firmly attached to the posterior abdominal wall. The small intestine commences by a dilated portion eight or ten inches in length, called the duodenum. The remainder is divided into the jejunum and the ileum. The former embraces the upper two-fifths of the intestine, but there is no distinct line of separation between it and the ileum. The mucous membrane lining the small intestine is thick, provided with an immense number of villi, and, particularly in the upper portion, is thrown into transverse folds, which are called the valvulæ conniventes. The valvulæ conniventes disappear in the lower part of the ileum. They are peculiar to the human subject. Thickly set in the upper part of the duodenum and scattered through its lower portion and the upper part of the jejunum, are small compound follicles called the glands of Brunner; and throughout the whole of the intestine are simple follicles, called the follicles of Lieberkühn. These glandular organs secrete the intestinal juice. As the food passes from the stomach into the intestine, it imbibes the bile and pancreatic juice, which are poured into the duodenum, as well as the intestinal juice.

Between the mucous membrane of the small intestine and the peritoneum, are two layers of unstriped muscular fibres, by the progressive peristaltic action of which the food is passed slowly on toward the large intestine. The alimentary principles, liquefied and prepared by digestion, are gradually absorbed by the blood-vessels of the intestinal mucous membrane and by the lacteals.

The indigestible residue of the food is passed by peristaltic action into the large intestine. This portion of the alimentary canal is from four to six feet in length; and, like the small intestine, it has a peritoneal, mucous, and muscular coat. Under ordinary conditions the large intestine is not concerned in digestion. It simply retains the residue of food, with certain excrementitious substances, until its contents are expelled by the act of defæcation.

Prehension of Solids and Liquids.

The different modes of prehension form a very interesting part of the physiology of digestion in the inferior animals; but, in the human subject, the process is so simple and well known that it demands nothing more than a passing mention. The mechanism of sucking in the infant and of drinking is a little more complicated. In sucking, the lips are closed around the nipple, the velum pendulum palati is applied to the back of the tongue so as to close the buccal cavity posteriorly, and the tongue, acting as a piston, produces a tendency to a vacuum in the mouth, by which the liquids are drawn in with considerable force. This may be done independently of the act of respiration, which is necessarily arrested only during deglutition; for the mere act of suction has never any thing to do with the condition of the thoracic walls. The mechanism of drinking from a vessel is essentially the same. The vessel is inclined so that the lips are kept covered with the liquid and are closed around the edge. By a gentle, sucking action the liquid is then introduced. This is the ordinary mechanism of drinking; but sometimes the head is thrown back and the liquid is poured into the mouth, as in "tossing off" the contents of a small vessel as a wine-glass.

Mastication.

In the human subject, mechanical division of food in the mouth is neither so completely and laboriously effected as in the herbivora, particularly the ruminants, nor is the process so rapid and imperfect as in the carnivora. In order that digestion may take place in a perfectly natural manner, it is necessary that the food, as it is received into the stomach, should be so far comminuted and incorporated with the fluids of the mouth as to be readily acted upon by the gastric juice; otherwise stomach-digestion is prolonged and difficult. Non-observance of this physiological law is a frequent cause of what is generally called dyspepsia. In animals that do not masticate, as in some which live exclusively on flesh, the process of stomach-digestion is much more prolonged than in the human subject, even when the diet is the same; and it is found that while man must, as a rule, take food two or three times in the day, the carnivorous animals are generally best nourished when food, in proper quantity, is taken but once in the twenty-four hours. In the carnivora, the proportionate quantity of food is greater than in man, and digestion is much more prolonged.

The comparative anatomy of the organs of mastication makes it evident that the human race is designed to live on a mixed diet; but experience has shown that man can be nourished for an indefinite period on a diet composed exclusively of either animal or vegetable principles.

Physiological Anatomy of the Organs of Mastication.—In the adult, each jaw is provided with sixteen teeth, all of which are about equally well developed. The canines, so largely developed in the carnivora but which are rudimentary in the herbivora, and

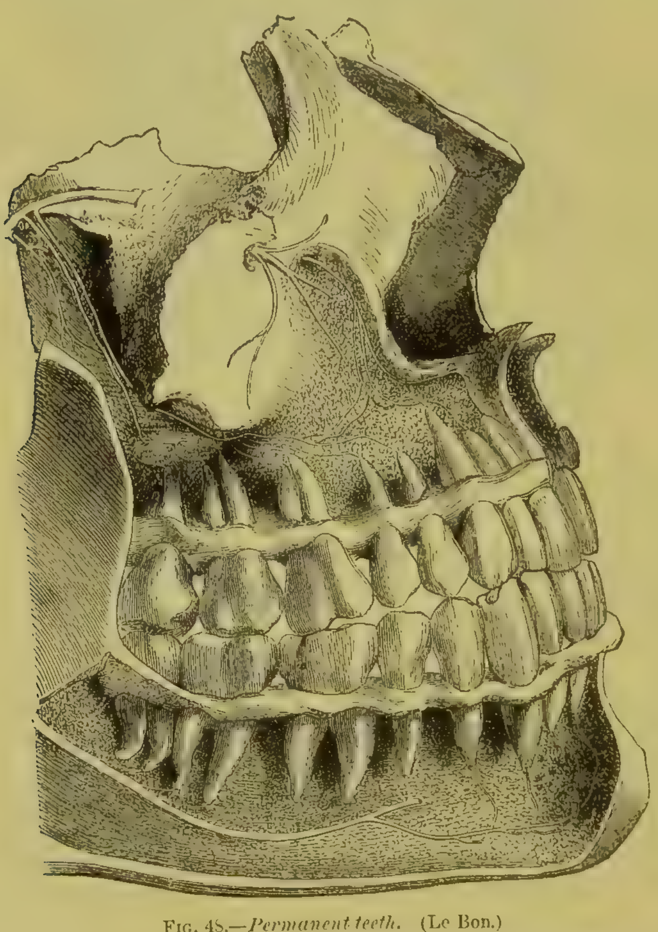


FIG. 48.—*Permanent teeth.* (Le Bon.)
The external portions of the maxillary bones have been removed to show the roots of the teeth.

the incisors and molars, so perfectly developed in the herbivora, are, in man, of nearly the same length. Each tooth presents for anatomical description a crown, a neck, and a root, or fang. The crown is that portion which is entirely uncovered by the gums; the root is that portion embedded in the alveolar cavities of the maxillary bones; and the neck is the portion, sometimes slightly constricted, situated between the crown and the root, covered by the edge of the gum. Thin sections of the teeth show that they are composed of several distinct structures.

Enamel of the Teeth.—The crown is covered by the enamel, which is by far the hardest structure in the economy. This is white and glistening and is thickest on the lower portion of the tooth, especially over the surfaces which, from being opposed to each other on either jaw, are most exposed to wear. It here exists in several concentric layers. The incrustation of enamel becomes gradually thinner toward the neck, where it ceases. Microscopical examination shows that the enamel is made up of pentagonal or hexagonal rods, one end resting upon the subjacent structure, and the other, when there exists but a single layer of enamel, terminating just beneath the cuticle of the teeth. The hardness of the enamel varies in different persons. In some it is so soft that in middle life it becomes worn away from the opposing surfaces, and occasionally the teeth are worn down almost to the gums; while in others the enamel remains over the crown of the tooth even in old age.

The exposed surfaces of the teeth are still farther protected by a membrane, from $\frac{1}{30000}$ to $\frac{1}{15000}$ of an inch in thickness, closely adherent to the enamel, called the cuticle of the enamel. This delicate membrane may be demonstrated in thin sections of young teeth by the addition, under the microscope, of weak hydrochloric acid. The acid attacks the enamel, producing little bubbles of gas which press out the membrane from the edge of the preparation and thus render it apparent. The cuticle presents a strong resistance to reagents and is undoubtedly very useful in protecting the teeth from the action of acids which may find their way into the mouth.

Dentine.—The largest portion of the teeth is composed of a peculiar structure called dentine, or ivory. In many respects, particularly in its composition, this resembles bone; but it is much harder, and does not possess the lacunæ and canaliculi which are characteristic of the true osseous structure. The dentine bounds and encloses the central cavity of the tooth, extending in the crown to the enamel and in the root, to the cement. It is formed of a homogeneous fundamental substance, which is penetrated by an immense number of canals radiating from the pulp-cavity toward the exterior. These are called the dentinal tubules or canals. They are from $\frac{1}{25000}$ to $\frac{1}{12000}$ of an inch in diameter, with walls of a thickness a little less than their caliber. Their course is slightly wavy or spiral. Commencing at the pulp-cavity, into which these canals open by innumerable little orifices, they are found to branch and occasionally anastomose, their communications and branches becoming more numerous as they approach the external surface of the tooth. The canals of largest diameter are found next the pulp-cavity, and they become smaller as they branch. The structure which forms the walls of these tubules is somewhat denser than the intermediate portion, which is sometimes called the inter-tubular substance of the dentine; but, in some portions of the tooth, the tubules are so numerous that their walls touch each other, and there is, therefore, no inter-tubular substance. Near their origin and near the peripheral terminations of the dentinal tubules, are sometimes found solid globular masses of dentine, called dentine-globules, which irregularly bound triangular or stellate cavities of very variable size. These cavities have been considered as lacunæ, like the lacunæ of true bone; but this view is not held by the best and most recent observers. Sometimes these cavities are very numerous and form regular zones near the peripheral termination of the tubules. The dentine is sometimes marked by concentric lines, indicating a lamellated arrangement. In the natural condition, the dentinal tubules are filled with a clear liquid, which penetrates from the vascular structures in the pulp-cavity.

Cement.—Covering the dentine of the root, is a thin layer of true bony structure, called the cement, or crusta petrosa. This is thickest at the summit and the deeper portions of the root, where it is sometimes lamellated, and it becomes thinner near the neck. It finally becomes continuous with the enamel of the crown, so that the dentine is everywhere completely covered. The cement contains true bone-lacunæ and canaliculi, and, in very old teeth, a few Haversian canals, except near the neck, where the layer is very thin. It is closely adherent to the dentine and to the periosteum lining the alveolar cavities.

Pulp-Cavity.—In the interior of each tooth, extending from the apex of the root or roots into the crown, is the pulp-cavity, which contains a collection of minute blood-vessels and nervous filaments, held together by longitudinal fibres of white fibrous tissue. This is the only portion of the tooth endowed with sensibility. Its blood-vessels and nerves penetrate by a little orifice at the extremity of the root.

The dentine and enamel of the teeth must be regarded as perfected structures; for, when the second or permanent teeth are lost, they are never reproduced, and when these parts are invaded by wear or by decay, they are incapable of regeneration. The integrity of the pulp, even, is not necessary to the stability of the teeth; for examples are numerous in which the pulp loses its vitality from various causes, and yet the tooth remains and is as serviceable as ever, being only discolored by the decomposition of the structures in the pulp-cavity, which can neither escape nor become absorbed.

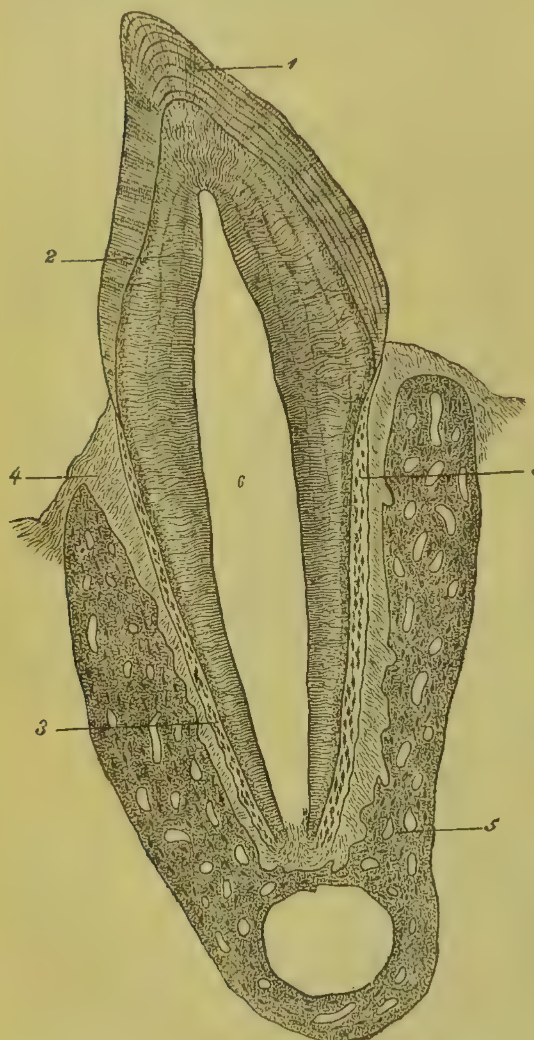


Fig. 49.—*Tooth of the cat, in situ.* (Waldeyer.)
1, enamel; 2, dentine; 3, cement; 4, periosteum of the alveolar cavity; 5, lower jaw; 6, pulp-cavity.

The descriptive anatomy of the teeth in the human subject shows how well calculated they are to perform their varied functions, and how admirably they are adapted to a diet composed of articles derived from both the animal and the vegetable kingdom. The thirty-two permanent teeth are divided as follows:

1. Eight incisors, four in each jaw, called the central and lateral incisors.

2. Four canines, or cuspidati, two in each jaw, just back of the incisors. The upper canines are sometimes called the eye-teeth, and the lower canines, the stomach-teeth.

3. Eight bicuspid—the small, or false molars—just back of the canines; four in each jaw.

4. Twelve molars, or multicuspid, situated just back of the bicuspid; six in each jaw.

The incisors are wedge-shaped, flattened antero-posteriorly, and bevelled at the expense of the posterior face, giving them a sharp, cutting edge, which is sometimes perfectly straight but is generally more or less rounded. The upper incisors are generally larger and stronger than the lower. In the upper jaw the central incisors are larger than the lateral; while in the lower jaw the lateral incisors are larger than the central. Each of the incisors has but a single root. The special function of the incisor teeth is to divide the food as it is taken into the mouth. The permanent incisors make their appearance from the seventh to the eighth year.

The canines are more conical and pointed than the incisors and have longer and larger roots, especially those in the upper jaw. Their roots are single. They are used to some extent, in connection with the incisors, in dividing the food; but they have no prominent function in tearing the food, as in the carnivora, in which they are extraordinarily developed. The permanent canines make their appearance from the eleventh to the twelfth year.

The bicuspid teeth are shorter and thicker than the canines. Their opposed surfaces are rather broad and are marked by two eminences. The upper bicuspids are somewhat larger than the lower. The roots are single, but in the upper jaw they are slightly bifurcated at their extremities. They are used, with the true molars, in triturating the food. The permanent bicuspids make their appearance from the ninth to the tenth year.

The molar teeth, called respectively—counting from before backward—the first, second, and third molars, are the largest of all and are, *par excellence*, the teeth used in mastication. Their form is that of a cube, rounded laterally and provided with four or five eminences on their opposed surfaces. The first molars are the largest. They have generally three roots in the upper jaw and two in the lower, although they sometimes have four or even five roots. The second molars are but little smaller than the first and resemble them in nearly every particular. The third molars, called frequently the wisdom-teeth, are much smaller than the others and are by no means so useful in mastication. In the upper jaw the root is grooved or imperfectly divided into three branches; but in the lower jaw it generally has two distinct branches. The first molars are the first of the permanent teeth, making their appearance between the sixth and the seventh year. The second molars appear from the twelfth to the thirteenth year; and the third molars, from the seventeenth to the twenty-first year, and sometimes even much later. In some instances the third molars are never developed.

The upper jaw has ordinarily a somewhat longer and broader arch than the lower; so that when the mouth is closed the teeth are not brought into exact apposition, but the upper teeth overlap the lower teeth both in front and laterally. The lower teeth are all somewhat smaller than the corresponding teeth in the upper jaw and generally make their appearance a little earlier.

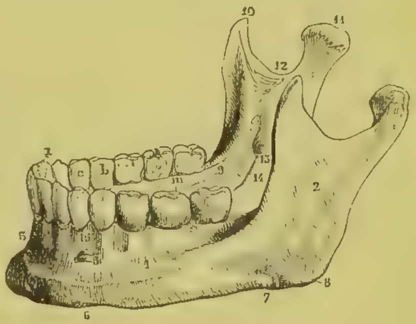


FIG. 50.—*Inferior maxilla.* (Sappey.)

1, body; 2, ramus; 3, symphysis; 4, incisive fossa; 5, mental foramen; 6, attachment of the digastric muscle, 7, depression at the site of the facial artery; 8, angle; 9, attachment of the superior constrictor of the pharynx; 10, coronoid process; 11, condyle; 12, sigmoid notch; 13, opening of the inferior dental canal; 14, groove for the mylo-hyoid muscle; 15, alveolar border; i, incisor teeth; c, canine teeth; b, bicuspid teeth; m, molars.

The physiological anatomy of the maxillary bones and of the temporo-maxillary articulation necessarily precedes the study of the muscles of mastication and the mechanism of their action.

The superior maxillary bones are immovably articulated with the other bones of the head and do not usually take any active part in mastication; but their inferior borders, with the upper teeth embedded in the alveolar cavities, present fixed surfaces against which the food is pressed by the action of the muscles which move the lower jaw.

The inferior maxilla is a single bone. Its body is horizontal, of a horseshoe shape, and, in the alveolar cavities in its superior border, are embedded the lower teeth. Below the teeth, both externally and internally, are surfaces for the attachments of the muscles concerned in the various movements of the jaw, and for one of the muscles of the tongue.

Behind the body of the inferior maxilla, on either side, is a vertical portion called the ramus. In the adult, this forms nearly a right angle with the body, making what is called the angle of the jaw. Superiorly, the ramus terminates in two processes, separated by a deep groove called the sigmoid notch. The posterior process is the condyle, or condyloid process, the anatomy of which will be considered farther on in treating of the temporo-maxillary articulation. The anterior process, called the coronoid process, is for the attachment of the temporal muscle, one of the most powerful of the muscles of mastication. The greater portion of the external surface of the ramus, extending down to the angle, is for the attachment of the masseter muscle. The internal surface of the ramus gives attachment to several muscles; viz., the external pterygoid, attached to the neck just below the condyle, the temporal, the attachment to the coronoid process being much more extensive on the internal than on the external surface, and the internal pterygoid, which has its attachment at the angle.

Temporo-Maxillary Articulation.—The various classes of mammalia present great differences in the temporo-maxillary articulation, differences which indicate, to a great extent, their natural diet. In the carnivora, the long diameter of the condyle is transverse, and it is so firmly embedded in the deep glenoid cavity of the temporal bone as to admit of extended movements in but one direction. In these animals, lateral and antero-posterior sliding movements of the jaw are impossible, and there is very little mastication of the food. In the rodentia, the long diameter of the condyle is antero-posterior, the peculiar gnawing movements in these animals requiring a considerable sliding movement of the lower jaw in this direction. In the herbivora, particularly the ruminants, the condyle is small and slightly concave instead of convex as in most other animals. It moves on a large projecting surface on the temporal bone, and the entire jaw is capable of remarkably extensive lateral movements.

In man, the articulation of the lower jaw with the temporal bone is such as to allow, to a considerable extent, of an antero-posterior sliding movement and a lateral movement, in addition to the ordinary movements of elevation and depression. The condyloid process is convex, with an ovoid surface, the general direction of its long diameter being transverse and slightly oblique from without inward and from before backward. This process is received into a cavity of corresponding shape in the temporal bone, called the glenoid fossa, which is bounded, anteriorly, by a rounded eminence (eminentia articularis), the uses of which will be more fully described in connection with the movements of the jaw.

Between the condyle of the lower jaw and the glenoid fossa, is an oblong, inter-articular disk of fibro-cartilage. This disk is thicker at the edges than in the centre. It is pliable and so situated that when the lower jaw is projected forward, making the lower teeth project beyond the upper, it is applied to the convex surface of the eminentia articularis and presents a concave surface for articulation with the condyle. One of the uses of this cartilage is to constantly present a proper articulating surface upon the articular eminence and thus admit of the antero-posterior sliding movement of the lower jaw. It is also important in the lateral movements of the jaw, in which one of the condyles remains in the glenoid cavity and the other is projected, so that the bone undergoes a slight rotation.

Muscles of Mastication.—To the lower jaw are attached certain muscles, by which it is depressed, and others by which it is elevated, projected forward and drawn backward, and moved from side to side. The following are the principal muscles concerned in the production of these varied movements:

Muscles of Mastication.

Muscles which depress the lower jaw.

Muscle.	*Attachments.*
Digastric	Mastoid process of the temporal bone—Lower border of the inferior maxilla near the symphysis, with its central tendon held to the side of the body of the hyoid bone.

Muscle.	*Attachments.*
Mylo-hyoid	Body of the hyoid bone—Mylo-hyoid ridge on the internal surface of the inferior maxilla.
Genio-hyoid	Body of the hyoid bone—Inferior genial tubercle on the inner surface of the inferior maxilla near the symphysis.
Platysma myoides	Clavicle, acromion, and fascia—Anterior half of the body of the inferior maxilla near the inferior border.

Muscles which elevate the lower jaw and move it laterally and antero-posteriorly.

Temporal	Temporal fossa—Coronoid process of the inferior maxilla.
Masseter	Malar process of the superior maxilla, lower border and internal surface of the zygomatic arch—Surface of the ramus of the inferior maxilla.
Internal pterygoid	Pterygoid fossa—Inner side of the ramus and angle of the inferior maxilla.
External pterygoid	Pterygoid ridge of the sphenoid, the surface between it and the pterygoid process, external pterygoid plate, and the tuberosity of the palate and the superior maxillary bone—Inner surface of the neck of the condyle of the inferior maxilla and the inter-articular fibro-cartilage.

Action of the Muscles which depress the Lower Jaw.—The most important of these muscles have for their fixed point of action the hyoid bone, which, under these circumstances, is fixed by the muscles which extend from it to the upper part of the chest. The central tendon of the digastric, as it perforates the stylo-hyoid, is connected with the hyoid bone by a loop of fibrous tissue; and, acting from this bone as the fixed point, the anterior belly must of necessity tend to depress the jaw. The attachments of the mylo-hyoid and the genio-hyoid render their action in depressing the jaw sufficiently evident, which is also the case with the platysma myoides, acting from its attachments to the upper part of the thorax.

It has been a disputed question whether the upper jaw does or does not participate in the act of opening the mouth. That depression of the lower jaw is the main action in ordinary mastication is sufficiently evident; but it is possible, by fixing the lower jaw, to perform the acts of mastication—laboriously and imperfectly it is true—by movements of the upper jaw. In ordinary mastication, however, the upper jaw undergoes a slight movement of elevation in opening the mouth; and this becomes somewhat exaggerated when the mouth is opened to the fullest possible extent.

Action of the Muscles which elevate the Lower Jaw and move it laterally and antero-posteriorly.—The temporal, masseter, and internal pterygoid muscles are chiefly concerned in the simple act of closing the jaws. As this is almost the only movement of mastication in many of the carnivora, in this class of animals these muscles are most largely developed. Their anatomy alone gives a sufficiently clear idea of their mode of action; and their immense power, even in the human subject, is explained by the number of their fibres, by the attachments of many of these fibres to the strong aponeuroses by which they are covered, and the fact that the distance from their origin to their insertion is very short.

The attachments of the internal and external pterygoids are such that, by their alternate action on either side, the jaw may be moved laterally, as their points of origin are situated in front of and internal to the temporo-maxillary articulation. The articulation of the lower jaw is of such a nature that, in its lateral movements, the condyles themselves cannot be sufficiently displaced from side to side, but, with the condyle on one side fixed or moved slightly backward, the other may be brought forward against the articular eminence, producing a movement of rotation. The pterygoid muscles are largely developed in the herbivora, in which the lateral movements of mastication are so important.

The above explanation of the lateral movements of the jaw presupposes the possibility of movements in an antero-posterior direction. Movements in a forward direction, so as to make the lower teeth project beyond the upper, are effected by the pterygoids, the oblique fibres of the masseter, and the anterior fibres of the temporal. By the combined action of the posterior fibres of the temporal, the digastric, mylo-hyoid, and genio-hyoid, the jaw is brought back to its position. By the same action it may also be drawn back slightly from its normal position while at rest.

Action of the Tongue, Lips, and Cheeks, in Mastication.—Experiments on living animals and phenomena observed in cases of lesions of the nervous system in the human subject have fully demonstrated the importance of the tongue and cheeks in mastication. The following observations of Panizza on the effects of section of both hypoglossal nerves in dogs show the importance of the tongue, both in mastication and deglutition: "After the section of the hypoglossal the movements of the tongue cease immediately, but the general sensibility of that organ and the taste was not less marked. Indeed, if milk, or bread moistened in the liquid, were presented to the dog, he made ineffectual efforts to lap and to masticate, moving the head and the lower jaw; the tongue, when displaced, remaining in the same position, and even when a bolus of meat or bread was put on its anterior surface, it was found for a long time after in the same place, which proves that section of the hypoglossals destroys not only the movements necessary to mastication, but also those of deglutition." We have lately had occasion to verify most of these observations in a dog in which both sublingual nerves were divided. The experiment, however, was made chiefly with reference to the action of the tongue in deglutition.

Section of the facial nerves is now a common physiological experiment. Operations of this kind and cases of facial palsy, which are not uncommon in the human subject, show that when the cheek is paralyzed the food accumulates between it and the teeth, producing great inconvenience. In animals, like the herbivora, which use the lips and tongue extensively in the prehension of food, division of the facial and hypoglossal nerves interferes materially with this function.

The tongue is a muscular organ which, by virtue of the complex arrangement of its fibres, is capable of a great variety of important movements. By the action of what are called the extrinsic muscles of the tongue, the organ is moved in various directions, while the intrinsic muscles are capable at the same time of producing many changes in its form. For example, by the action of those fibres of the genio-hyo-glossal muscles which are attached to the chin and the posterior part of the tongue, the whole organ is carried forward and may be protruded to a considerable extent. At the same time the whole length of the muscles may act upon the middle line of the tongue, to which they are attached, and depress the centre so as to render it concave from side to side; or the transverse fibres of the tongue may act so as to make it longer and narrower. The tongue is drawn into the mouth by the action of the anterior fibres of the genio-hyo-glossus on either side, and may be still farther shortened by the contraction of the stylo-glossus and the inferior fibres of the hyo-glossus. The general action of the hyo-glossus, on either side, is to draw down the sides of the tongue and make it convex from side to side. The stylo-glossus and the palato-glossus draw the back of the tongue upward and backward toward the pharnyx, and they are thus useful in the first processes of deglutition. By the combined and varied actions of these and other muscles, the tongue is made to perform the numerous movements which take place in connection with phonation, suction, mastication, deglutition, etc.

The varied and complicated movements of the tongue during mastication are not easily described. After solid food is taken into the mouth, the tongue prevents its escape from between the teeth, and, by its constant movements, rolls the alimentary bolus over and over and passes it at times from one side to the other, so that the food may undergo thorough trituration. Aside from the functions of the tongue as an organ of taste, its surface is endowed with peculiar sensibility as regards the consistence, size, and form of different articles; and this property is undoubtedly important in determining when mastication is completed, although the thoroughness with which mastication is accomplished is very much influenced by habit.

Tonic contraction of the orbicularis oris is necessary to keep the fluids within the mouth during repose; and this muscle is sometimes brought into action when the mouth is very full, to assist in keeping the food between the teeth. This latter function, however, is mainly performed by the buccinator; the action of which is to press the food between the teeth and keep it in place during mastication, assisting, from time to time, in turning the alimentary bolus so as to subject new portions to trituration.

The process of mastication is regulated to a very great extent by the exquisite sensibility of the teeth to the impressions of hard and soft substances. It is only necessary to call attention to the ease and certainty with which we recognize the presence and the consistence of the smallest substance between the teeth, in order to appreciate the advantages of this tactile sense in mastication. It is in this way, mainly, that we become aware that the process of mastication is completed; and it is this sense which admonishes us instantly of the presence of bodies too hard for mastication, which, if allowed to remain in the mouth, might seriously injure the teeth.

One of the most important of the digestive processes which take place in the mouth is the incorporation of the saliva with the food, or insalivation. Not only has the saliva a mechanical function, assisting to reduce the food to the proper form and consistence to be easily swallowed, but it seems to be necessary to the proper performance of the subsequent processes of digestion and is concerned to a certain extent in the transformation of starch into sugar. That the saliva is necessary to digestion is proven by the grave effects upon the general function of nutrition which follow its loss in any considerable quantity. This occasionally occurs from the habit of excessive spitting or as the result of salivary fistula. It becomes important, therefore, to study the physical and chemical properties of the saliva, the sources from which it is derived, and its mechanical and chemical functions in digestion.

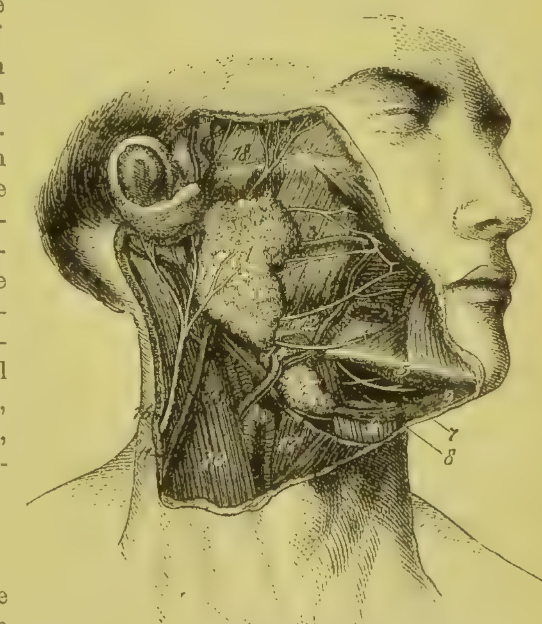


FIG. 51.—*Salivary glands.* (Le Bon.)

1, 2, *parotid*; 3, *duct of Steno*; 4, *submaxillary*; 5, *sublingual*; 6, mylo-hyoid muscle; 7, lingual branch of the fifth nerve; 8, *duct of Wharton*; 9, digastric muscle; 10, sterno-mastoid muscle; 11, external jugular vein; 12, facial vein; 13, temporal vein; 14, 15, internal jugular vein; 16, branch of the cervical plexus; 17, sublingual nerve.

Saliva.

The fluid which is mixed with the food in mastication, which moistens the mucous membrane of the mouth, and which may be collected at any time in small quantity by the simple act of sputation, is composed of the secretions of a considerable number and variety of glands. The most important of these are the parotid, submaxillary, and sublingual, which are usually called the salivary glands. In addition, we have the labial and buccal glands, the follicular glands of the tongue and general mucous surface, and certain glandular structures in the mucous membrane of the pharynx. The liquid which becomes more or less incorporated with the food before it descends to the stomach, and which must be considered as the digestive fluid of the mouth, is known as the mixed saliva; but the study of the composition and properties of this fluid as a whole should be prefaced by a consideration of the different secretions of which it is composed.

The salivary glands belong to the variety of glands called racemose. They closely resemble the other glands belonging to this class, and their structure will be considered more particularly under the head of secretion.

Parotid Saliva.—The parotid is the largest of the three salivary glands. It is situated below and in front of the ear and opens by the duct of Steno into the mouth, at about the middle of the cheek. The papilla which marks the orifice of the duct is situated opposite the second large molar tooth of the upper jaw.

Numerous opportunities have presented themselves, in cases of salivary fistula, for the study of the properties of the pure parotid saliva in the human subject; and the situation of the duct of Steno, in the herbivora especially, is such that this fluid can easily be obtained by operations on the inferior animals. Prof. J. C. Dalton has obtained the pure parotid saliva from the human subject by simply introducing a silver tube, of from $\frac{1}{25}$ to $\frac{1}{20}$ of an inch in diameter, into the duct by its opening into the mouth.

The following facts with regard to the properties of the parotid saliva observed by Dalton are given in his own words, in a communication kindly made in answer to certain inquiries:

"On the 28th of July, 1863, I obtained, from a strong, healthy man, about two drachms of the mixed saliva of the mouth, by causing him to hold in his mouth for a short time a clean glass stopper, and collecting the secretion as it was discharged.

"One hour afterward I obtained, from the same man, four drachms of pure parotid saliva, by introducing a long silver canula into the natural orifice of Steno's duct, on the left side, and collecting the saliva as it flowed from the outer extremity of the canula.

"The two kinds of saliva compared as follows:

"Both were distinctly alkaline in reaction; the parotid saliva rather the more so.

"The parotid saliva was rather clear and watery in appearance; the saliva of the mouth was quite opaline, with admixture of buccal epithelium, but became clear on filtration.

"The parotid saliva was rendered turbid by the action of heat, and by the addition of nitric acid, as well as sulphate of soda in excess; but not by sulphate of magnesia, nor by ferro-cyanide of potassium with acetic acid.

"The saliva of the mouth, filtered clear, became turbid by heat and by nitric acid, but showed no precipitate by either sulphate of soda or sulphate of magnesia in excess. There was also a slight precipitate on the addition of pure acetic acid, which did not take place in the parotid saliva.

"The parotid saliva showed no traces of sulpho-cyanogen on the addition of the perchloride of iron, but they were distinctly marked in the buccal saliva.

"On mixing the two kinds of saliva with boiled starch, and keeping the mixture at the temperature of 100° Fahr., sugar was present in both specimens at the end of five minutes. There was no marked difference between them in this respect.

"While making some similar experiments to the above on a previous patient, in April, 1863, I found that with the canula introduced into Steno's duct, not only was the discharge of parotid saliva increased by the mastication of food, but that it ran from the canula very much faster than in a state of rest, whenever the patient smiled, spoke, or moved his lips or cheeks in any way."

The organic matter of the parotid saliva is coagulable by heat (212° Fahr.), alcohol, and the strong mineral acids. Dalton found, in the human saliva, that it was also coagulated by an excess of sulphate of soda; but Bernard states that, in the parotid saliva of the horse, the organic matter passed through a mixture of sulphate of soda but was coagulated by sulphate of magnesia. Almost all physiologists agree that this organic matter is not identical in its properties with albumen or with the peculiar principle described by Mialhe in the mixed saliva, under the name of animal diastase.

A compound of sulpho-cyanogen is now generally acknowledged to be a constant constituent of the parotid saliva. This cannot be recognized by the ordinary tests in the fresh saliva taken from the duct of Steno, but in the clear, filtered fluid which passes after the precipitation of the organic matter, there is always a distinct red color on the addition of the persulphate of iron. As this reaction is more marked in the mixed saliva, the methods by which the presence of a sulpho-cyanide is to be demonstrated will be considered in connection with that fluid.

In the human subject, the parotid secretion is more abundant than that of any other of the salivary glands. The entire quantity in the twenty-four hours has not been directly estimated; but Prof. Dalton found that, during mastication, the quantity secreted in twenty minutes on one side was 127·5 grains, and on the other side, 374·4 grains.

A curious fact with regard to the influence of mastication upon the flow from the parotids was observed by Colin in the horse, ass, and ox. He found that, when mastication was performed on one side of the mouth, the flow from the gland on that side was greatly increased, exceeding by several times the quantity produced upon the opposite side. This fact was confirmed by Dalton, as already indicated, in the human subject.

The flow of saliva from the parotid takes place with greatly-increased activity during the process of mastication. The orifice of the parotid duct is so situated that the fluid is poured directly upon the mass of food as it is undergoing trituration by the teeth; and, as the secretion is more abundant on the side on which mastication is going on, and the consistence of the fluid is such as to enable it to mix readily with the food, the function of this gland is supposed to be particularly connected with mastication. This is undoubtedly the fact; although its flow is not absolutely confined to the period of mastication, but continues, in small quantity, during the intervals. Its quantity is regulated somewhat by the character of the food, being much greater when the articles taken into the mouth are dry than when they contain considerable moisture. There is a great difference in different animals as regards the stimulation of the salivary glands by substances introduced into the mouth. In the human subject, the stimulus produced by sapid substances will sometimes induce a great increase in the flow of the parotid saliva. Mitscherlich and Eberle observed this in persons suffering from salivary fistula and noted, farthermore, that the mere sight or odor of food produced the same effect.

The supposition, which has been entertained by some authors, that the flow from the parotid is dependent upon the mechanical pressure of the muscles or of the condyle of the lower jaw during mastication has no foundation in fact. It is now well established that one of the indispensable conditions in the production of a secretion is a great increase in the quantity of blood circulating in the gland, and that the vascular supply is regulated through the nervous system. The fact that an alternation in the parotid secretion accompanies an alternation in the act of mastication is also an argument against this mechanical theory; for it is not to be supposed that during mastication there exists a difference in the pressure of the muscles or of the condyles on the two sides, corresponding with the differences which have been noted in the secretion from the glands on either side. In the horse and in the dog, it has been observed that the secretion of the parotids is completely arrested during the deglutition of liquids, while the flow from the other salivary glands is not affected.

To sum up the functions of the parotid saliva—aside from any chemical action which it may have upon the food, which will be fully considered in connection with the mixed saliva—it evidently has an important mechanical office. It is discharged in large quantity during the entire process of mastication and is poured into the mouth in such a manner as to become of necessity thoroughly incorporated with the food. Its function is chiefly, although not exclusively, connected with mastication and indirectly, with deglutition; for it is only by becoming incorporated with this saliva, that the deglutition of dry, pulverulent substances is rendered possible. Facts in comparative physiology, showing a great development of the parotids in animals that masticate very thoroughly, particularly the ruminants, a slight development in those that masticate but slightly, and the absence of these glands in animals that do not masticate at all, are additional arguments in favor of these views.

Submaxillary Saliva.—In the human subject, the submaxillary is the second of the salivary glands in point of size. Its minute structure is the same as that of the parotid. As its name implies, it is situated below the inferior maxillary bone. It is in the anterior part of what is known as the submaxillary triangle of the neck. Its excretory duct, called sometimes the duct of Wharton, is about two inches in length and passes from the gland, beneath the tongue, to open by a small papilla by the side of the frenum. This gland is relatively very small in the herbivora but is largely developed in the carnivora, in the latter being larger than the parotid.

The pure submaxillary saliva presents many important points of difference from the secretion of the parotid. It was first studied as a distinct fluid by Bernard. It may be obtained by exposing the duct and introducing a fine silver tube, when, on the introduction of any sapid substance into the mouth, the secretion will flow in large, pearly drops. Bernard found this variety of saliva much more viscid than the parotid secretion. It is perfectly clear, and, on cooling, frequently becomes of a gelatinous consistence. Its organic matter is not coagulable by heat. In the dog, it is rather more strongly alkaline than the parotid saliva. According to Bernard, it does not contain the sulpho-cyanide of potassium.

The submaxillary gland pours out its secretion in greatest abundance when sapid substances are introduced into the mouth. In the solipeds and ruminants, Colin has observed that the quantity of submaxillary saliva secreted is much increased during eating; but, unlike the parotids, the secretion does not alternate on the two sides with the alternation in mastication. He has found, in all the domestic animals, that the flow is greatly influenced by the degree of sapidity of the food. Although sapid articles induce an abundant secretion from the submaxillary glands, they also produce an increase in the secretions from the parotids and sublinguals; and, on the other hand, movements of mastication increase somewhat the flow from the submaxillaries, and these glands secrete a certain amount of fluid during the intervals of digestion. The viscid consistence of the submaxillary saliva renders it less capable of penetrating the alimentary mass during mastication than the parotid secretion, so that it remains chiefly near the surface of the alimentary mass.

Sublingual Saliva.—The sublinguals, the smallest of the salivary glands, are situated beneath the tongue, on either side of the frenum. In minute structure they resemble the parotid and the submaxillary glands. Each gland has a number of excretory ducts, from eight to twenty, which open into the mouth by the side of the frenum; and one of the ducts, larger than the others, joins the duct of the submaxillary gland near its termination in the mouth.

The secretion of the sublingual glands is more viscid even than the submaxillary saliva, but it differs in the fact that it does not gelatinize on cooling. It is so glutinous that it adheres strongly to any vessel and flows with difficulty from a tube introduced into the duct. Like the secretion from the other salivary glands, its reaction is distinctly alkaline. Its organic matter is not coagulable by heat, acids, or the metallic salts. According to Bernard, after desiccation it is redissolved by water and its viscid properties are then restored.

In accordance with the view entertained by Bernard concerning the function of this variety of saliva and its special connection with deglutition, it is supposed to be secreted immediately before and during the act of swallowing. The experiments which are advanced in support of this view are mostly those in which a tube was fixed in each of the three salivary ducts in a dog, when the animal was caused to make movements of the jaw, movements of deglutition, and at the same time the gustatory nerves were stimulated by the introduction of vinegar into the mouth. In an experiment of this kind, it was observed that fluid was secreted by all the glands, but in unequal proportions; "the submaxillary saliva flowed very abundantly, the parotid saliva much less, and the sublingual saliva flowed very feebly." Although the animal made movements of mastication, experienced a gustatory impression, and made movements of deglutition, it is by no means evident from this observation, or from others reported by Bernard, that the flow of the sublingual saliva had any special connection with the act of deglutition. The observations of Colin on this subject show that, in the domestic ruminants, there is a constant flow of the sublingual saliva during the time occupied in eating.

It has been experimentally demonstrated that the sublingual glands may be excited to secretion by impressions made by sapid substances upon the nerves of taste, although the flow is always less than from the submaxillary glands. The great viscidity of the sublingual saliva renders it less easily mixed with the alimentary bolus than the secretions from the parotid or the submaxillary glands.

Fluids from the Smaller Glands of the Mouth, Tongue, and Pharynx.—Beneath the mucous membrane of the inner surface of the lips, are small, rounded, glandular bodies, opening by numerous ducts into the buccal cavity, called the labial glands; and, in the submucous tissue of the cheeks, are similar bodies, called the buccal glands. The latter are somewhat smaller than the labial glands. Two or three of the buccal glands are of considerable size and have ducts opening opposite the last molar tooth. These are sometimes distinguished as the molar glands. There are also a few small glands in the mucous membrane of the posterior half of the hard palate; but the glands on the under surface of the soft palate are larger and more numerous and here form a continuous layer. The glands of the tongue (lingual glands) are situated beneath the mucous membrane, mainly on the posterior third of the dorsum; but a few are found at the edges and the tip. All of these are small, racemose glands, similar in structure to those which have been called the true salivary glands. In addition to these structures, the mucous membrane of the tongue is provided with a number of simple and compound follicular glands, which extend over its entire surface but are most abundant at the posterior portion, behind the circumvallate papillæ.

In the pharynx and the posterior portion of the buccal cavity, are found the pharyngeal glands and the tonsils. In the pharynx, particularly the upper portion, racemose glands, like those found in the mouth, exist in large numbers. The mucous membrane is provided, also, with numerous simple and compound mucous follicles. The tonsils, situated on either side of the fauces between the pillars of the soft palate, consist of an aggregation of compound follicular glands, held together by fibrous tissue. The number of glands entering into the composition of each tonsil is from ten to twenty.

The secretion from the glands and follicles above enumerated cannot be obtained, in the human subject, unmixed with the fluids from the true salivary glands. It has been obtained, however, in small quantity, from the inferior animals, after ligature of all the salivary ducts. This secretion is simply a grayish, viscid mucus, containing a number of leucocytes and desquamated epithelial scales. It is this which gives the turbid and opaline character to the mixed saliva, as the secretions of the various salivary glands are all perfectly transparent. The fluid from these glands in the mouth is mixed with the salivary secretions; and that from the posterior part of the tongue, the tonsils, and the pharyngeal glands passes down to the stomach with the alimentary bolus. This secretion, consequently, forms a constant and essential part of the mixed saliva.

Mixed Saliva.—Although the study of the distinct secretions discharged into the mouth possesses considerable physiological interest and importance, it is only the fluid resulting from a union of them all, which can properly be considered in connection with the general process of insalivation. In man it is necessary that the cavity of the mouth should be continually moistened, if for nothing else, to keep the parts in a proper condition for phonation. A little reflection will make it apparent that the flow, from some of the glands at least, is constant, and that, from time to time, a certain quantity of saliva is swallowed. This is even more marked in some of the inferior animals, as the ruminants. The discharge of fluid into the mouth, though diminished, is not arrested during sleep. In the review of the different kinds of saliva, it has been seen that the flow from none of the glands is absolutely intermittent; unless it be so occasionally from the parotid, the secreting function of which is most powerfully influenced by the act of mastication and the impression of sapid substances.

Upon the introduction of food, the quantity of saliva is enormously increased; and we have already noted the influence of the sight, odor, and occasionally even the thought of agreeable articles. Many persons present a marked increase in the flow of saliva at the sight of a lemon; and we are all familiar, in a general way, with the impressions which bring "water into the mouth." The experiments of Frerichs on dogs with gastric fistulæ, and the observations of Gardner on a patient with a wound in the œsophagus, have demonstrated that the flow of saliva may be excited by the stimulus of food introduced directly into the stomach without passing through the mouth.

Quantity of Saliva.—It is not easy to estimate, in the human subject, the entire quantity of saliva secreted in the twenty-four hours; and great variations in this regard undoubtedly exist in different persons, and even in the same individual at different times. An approximate estimate may be arrived at by noting, as nearly as possible, the average quantity secreted during the intervals of digestion and adding to it the quantity absorbed by the various articles of food. Some of the earlier physiologists investigated this subject with much patience. Bérard quotes the experiments of Siebold, who collected the saliva by holding the mouth open with the head inclined, receiving the fluid in a vessel as fast as it was secreted. An estimate of this kind can only be approximative, and those made by Dalton are apparently the most satisfactory. This observer found that he was able to collect from the mouth, without any artificial stimulus, about five hundred and fifty-six grains of saliva per hour; and he also found that wheaten bread gained in mastication fifty-five per cent., and lean meat, forty-eight per cent. in weight. Assuming the daily allowance of bread to be nineteen ounces and the allowance of meat to be sixteen ounces, and estimating the quantity of saliva secreted during twenty-two hours of interval, the entire quantity in twenty-four hours would amount to 20,164 grains, or a little less than three pounds avoirdupois, of which rather more than one-half is secreted during the intervals of eating.

Remembering that the quantity of saliva must necessarily be subject to great variations, this estimate may be taken as giving a sufficiently close approximation of the quantity of saliva ordinarily secreted. It must be borne in mind, however, with reference to this and the other digestive secretions, that this immense quantity of fluid is at no one time removed from the blood, but is reabsorbed nearly as fast as secreted, and that, normally, none of it is discharged from the organism.

General Properties and Composition of Saliva.—The mixed fluid taken from the mouth is colorless, somewhat opaline, frothy, and slightly viscid. It generally has a faint and somewhat disagreeable odor very soon after it is discharged. If it be allowed to stand, it deposits a whitish sediment, composed mainly of desquamated epithelial scales, with a few leucocytes, leaving the supernatant fluid tolerably clear. Its specific gravity is variable, ranging from 1004 to 1006 or 1008. Its reaction is almost constantly alkaline; although, under certain abnormal conditions of the system, it has occasionally been observed to be neutral, and sometimes, though rarely, acid. We have occasionally observed a distinctly acid taste in the saliva after very severe, prolonged, and exhausting muscular exertion. The saliva becomes slightly opalescent by boiling or on the addition of the strong acids. The addition of absolute alcohol produces an abundant whitish, flocculent precipitate. Almost invariably the mixed saliva presents a more or less intense blood-red tint on the addition of a per-salt of iron, which is due to the presence of a sulpho-cyanide either of potassium or sodium.

A number of analyses of the human mixed saliva have been made by different chemists, presenting, however, few differences, except in the relative proportions of water and solid ingredients, which are probably quite variable. One of the most reliable of these analyses is the following, by Bidder and Schmidt:

Composition of Human Saliva.

Water	995·16
Epithelium	1·62
Soluble organic matter	1·34
Sulpho-cyanide of potassium	0·06
Phosphates of soda, lime, and magnesia	0·98
Chloride of potassium } Chloride of sodium }	0·84
	1,000·00

The organic principle of the mixed saliva, called by Berzelius ptyaline, is not affected by heat or the acids, but, on the addition of an excess of absolute alcohol, is coagulated in the form of whitish flakes, which may be readily separated by filtration. This substance has been closely studied by Mialhe and is described by him under the name of animal diastase. This author regards it as the active principle of the saliva. It is obtained from the human saliva by the following simple process:

The fluid from the mouth is first filtered, then treated with five or six times its weight of absolute alcohol, by which a white or grayish-white precipitate is formed. This substance is collected on a filter and is dried in thin layers on a plate of glass in a current of air at from 100° to 120° Fahr. It may then be preserved indefinitely in a well-stoppered bottle. The principle thus prepared may be dissolved in water, when it is insipid, neutral, and becomes readily decomposed, giving rise to a substance resembling butyric acid. It has no influence upon the nitrogenized alimentary principles, but, when brought in contact with raw or hydrated starch, readily transforms it, first into dextrine, and afterward into glucose. According to Mialhe, the energy of this action is such that one part is sufficient to effect the transformation of more than two thousand parts of starch.

The presence of a certain quantity of sulpho-cyanide of potassium in the mixed saliva can be demonstrated by the addition of a per-salt, especially the perchloride of iron. That this is a constant and normal ingredient of the human saliva cannot be doubted. We have frequently had occasion to apply this test to the saliva of different persons, and the results have been invariably the same.

It has been a question whether the red color produced by the perchloride of iron be really due to the presence of a sulpho-cyanide in the saliva; or, if it exist at all, whether this salt be a normal constituent or be developed accidentally as a pathological condition, or produced, as has been suggested, by the action of reagents. The elaborate investigations of Longet seem to have settled these questions conclusively. He obtained nearly three quarts of human saliva, which he collected in half an hour from forty soldiers, fasting, who, after having rinsed and cleaned the mouth, excited the secretion by chewing pieces of India-rubber. The fluid was then concentrated so that all the sulpho-cyanide was brought into a few drops, which showed, in an intense degree, the peculiar reaction with the perchloride of iron. By suitable manipulations, the presence of sulphur was also established.

Longet states, furthermore, that he has examined the saliva from a great number of persons, under all conditions, and has never failed to demonstrate the presence of the sulpho-cyanide. Its proportion he found very variable, and in some cases it was so slight that the reaction with the perchloride of iron did not immediately manifest itself; but, by slowly evaporating the liquid to one-half or one-third of its original volume, the reaction was observed in all cases.

It is probable that the sulpho-cyanide of potassium is a constant ingredient of each of the three varieties of saliva. It has been found in the parotid, in cases of salivary fistula, and was noted by Dalton in the saliva taken from the duct of Steno, although, in this case, the saliva contained an organic principle which interfered with the test, but which could be precipitated by alcohol and separated by filtration. Longet found the sulpho-cyanide in the saliva from the submaxillary and sublingual glands, taken from the floor of the mouth behind the inferior incisor and canine teeth.

Very little need be said concerning the remaining inorganic constituents of saliva, except that they are of such a nature as almost invariably to render the fluid distinctly alkaline. They exist in small proportion and do not appear to be connected in any way with the functions of the saliva as a digestive fluid.

Functions of the Saliva.

Physiologists are not entirely agreed concerning some of the most important questions relating to the function of the mixed saliva in digestion. Bernard, from observations on the lower animals, particularly on dogs, concludes that the operation of the saliva is simply mechanical; while others, in view of its property of rapidly transforming starch into sugar, attribute to it an important chemical function. The experiments on which the view of Bernard is based are conclusive, so far as they go. He has shown that none of the distinct varieties of saliva from the dog affect starch; that a mixture of the fluids from the three salivary glands is likewise inoperative; and that the mixed saliva from the mouth of the dog, containing the secretion of the mucous glands of the mouth, converts starch into sugar with difficulty. At the same time, however, he mentions the well-known fact that the human mixed saliva changes starch into sugar with great rapidity, and that the same effect is produced by the unmixed parotid or submaxillary secretion. In the dog, amylaceous principles taken by the mouth are always found unaltered in the stomach and are only transformed into sugar in the small intestines; but observations have shown that this is not the case in the human subject. These facts are a sufficient argument against the direct application of experiments made on an exclusively carnivorous animal, like the dog, to the digestive process in man. While there is no reason to suppose that there is any material difference in the mammalia, as regards the general operation of some of the functions, such as circulation or respiration, it is evident that differences exist in the properties of the digestive fluids, as well as in the teeth and jaws, corresponding with the great differences in the character and conditions of the alimentary principles. In the study of digestion, therefore, the results of experiments on the inferior animals cannot always be taken without reserve, and they should be confirmed by observations on the human subject; but, fortunately, the properties of nearly all of the digestive fluids which have been studied minutely by vivisections have been investigated more or less fully in man.

In 1831, Leuchs discovered that hydrated starch, mixed with fresh saliva and warmed, became liquid in the space of several hours and was converted into sugar. This fact has since been repeatedly confirmed; and it is now a matter of common observation that hydrated starch or unleavened bread, taken into the mouth, almost instantly loses the property of striking a blue color with iodine and responds to the ordinary tests for sugar. Of the rapidity of this action any one can easily convince himself by the simple experiment of taking a little cooked starch into the mouth, mixing it well with the saliva, and testing in the ordinary way for sugar. This can hardly be done so rapidly that the reaction is not manifested, and the presence of sugar is also indicated by the taste. Although the human mixed saliva will finally exert the same action on uncooked starch, the transformation takes place much more slowly. It has been shown by experiment that all the varieties of human saliva have the same effect on starch as the mixed fluids of the mouth. Dalton found no difference in the pure parotid saliva and the mixed saliva of the human subject, as regards the power of transforming starch into sugar. Bernard obtained the pure secretions from the parotid and from the submaxillary glands in the human subject, by drawing it out of the ducts, as they open into the mouth, with a small syringe with the nozzle arranged so as to fit over the papillæ, and demonstrated their action on starch. Longet showed that a mixture of the secretions of the submaxillary and the sublingual glands had the same property.

It is unnecessary, in this connection, to recite the numerous experiments on the influence of the saliva of the inferior animals on starch; but it may be stated, as an established and generally-accepted fact, that the mixed saliva and the secretion of the different salivary glands, in the human subject, invariably transform cooked starch into sugar with great rapidity in the mouth, and also, at the proper temperature, out of the body. It has been also shown by Mialhe that the starch, although it is converted rapidly into sugar in this process, is first transformed into dextrine. This point being settled, there arises the important question whether the action of the saliva be important in the digestion of starch, or whether this transformation be merely accidental; for it has been shown that other fluids, among which may be mentioned the serum of the blood, the fluid found in cysts, and mucus, have the same property, although none, except the intestinal juices, are nearly so efficient as the saliva. And, again, the quantity of starch contained in the food is so great that it would require, apparently, a longer contact with the saliva than usually takes place in the mouth to make this action very efficient. These considerations make it necessary to follow the amylaceous principles of food into the stomach and to ascertain, if possible, whether the transformation into sugar be continued in this organ.

Bernard, after feeding a dog with starch, drew off the contents of the stomach by a gastric fistula and found the starch unchanged, with no traces of sugar. This experiment we have often repeated in public demonstrations, with the same results; but the differences already noted in the properties of the saliva of the human subject and of the inferior animals destroy much of the value of such observations. Longet and others have shown that the addition of gastric juice to the saliva does not interfere with the action of the latter on starch, but it has been found that the reaction of the sugar thus resulting from the transformation of the starch is masked by the presence of other principles contained in the stomach. The question of the continuance, in the stomach, of the digestion of starch by the saliva is settled by the following observation by Grünewaldt and Schröder, in 1853, on a woman with a gastric fistula:

"After a meal of raw starch, no sugar was found in the contents of the stomach, the acid juice was drawn by the fistula, and was mixed with paste; the transformation into sugar commenced immediately. As Bidder has observed, the transforming property of the saliva persists, even in the presence of free acids.

"A few ounces of starch swelled with boiling watér were introduced in the stomach, fasting, by the fistula; immediately after, a portion of the starch was expelled again; already it contained sugar. A quarter of an hour after, a great deal of sugar was found in the stomach, and the paste had become entirely fluid."

There can be no doubt that the saliva, in addition to its important mechanical functions, transforms a considerable portion of the cooked starch, which is the common form in which this principle is taken by the human subject, into sugar; but it is by no means the only fluid engaged in its digestion, similar properties belonging, as we shall see hereafter, to the pancreatic and the intestinal juice. The last-named fluids are probably more active, even, than the saliva. The saliva acts slowly and imperfectly on raw starch, which becomes hydrated in the stomach and is digested mainly by the fluids of the small intestine. In all probability, the saliva does not digest all the hydrated starch taken as food, the greater part passing unchanged from the stomach into the intestine. Those who attribute merely a mechanical function to the saliva draw their conclusions entirely from experiments on the lower animals, particularly the carnivora; and it is evident that such observations cannot be strictly applied to the human subject.

The principle which is specially active in the digestion of starch, in the human subject at least, must exist in the pure secretion from the various glands as well as in the mixed saliva. It has been isolated and studied by Mialhe, under the name of animal diastase. Its properties and its action on starch have already been noted in treating of the composition of the mixed saliva.

In treating of the various fluids which are combined to form the mixed saliva, their mechanical functions have necessarily been touched upon. To sum up this subject, however, it may be stated that the fluids of the mouth and pharnyx have quite as important an office in preparing the food for deglutition and for the action of the juices in the stomach as in the digestion of starch. Indeed, the former is probably the more important function in man and the herbivora. It is a matter of common experience that the rapid deglutition of very dry articles is impossible; and the experiments of Bernard and others on horses furnish very striking illustrations of the importance of the saliva as a purely mechanical agent. In the human subject, although mastication and insalivation are by no means so complete as in some of the lower animals, the quantity of saliva absorbed by the various articles of food is enormous. It seems impossible that the fluid thus incorporated with the alimentary principles should not have an important influence on the changes which take place in the stomach, although it must be confessed that our information on this point is very meagre, except as regards the digestion of starch.

It is undoubtedly the abundant secretion of the parotid glands which becomes most completely incorporated with the food during mastication and which serves to unite the dry particles into a single coherent mass. In an experiment on a horse, Bernard found that, after the ducts of Steno had been divided, the portions of food, which were collected by an opening into the œsophagus as they were swallowed, were not coherent and were passed into the stomach with great difficulty. The time occupied in eating about three-quarters of a pound of oats was twenty-five minutes; while, before the section of the salivary ducts, a pound of oats was eaten in nine minutes.

The secretions from the submaxillary and sublingual glands and from the small glands and follicles of the mouth, being more viscid and less in quantity than the parotid secretion, penetrate the alimentary bolus less easily and have rather a tendency to form a glairy coating on its exterior, agglutinating the particles on the surface with peculiar tenacity.

When the process of mastication and insalivation is completed and the food is passed back into the pharynx, it meets with the secretion of the pharyngeal glands, which still farther coats the surface with the viscid fluid which covers the mucous membrane in this situation, thus facilitating the first processes of deglutition.

It has been observed that the saliva has a remarkable tendency to entangle bubbles of air in the alimentary mass. In mastication, a considerable quantity of air is mixed with the food, and this undoubtedly facilitates the penetration of the gastric juice. It is well known that moist, heavy bread, and articles that cannot become impregnated in this way with air, are not easily acted upon in the stomach.

Deglutition.

Deglutition is the act by which solid and liquid articles are forced from the mouth into the stomach. The process involves first, the passage, by a voluntary movement, of the alimentary mass through the isthmus of the fauces into the pharynx; then a rapid contraction of the constrictors of the pharynx, by which it is forced into the œsophagus;

and, finally, a peristaltic action of the muscular walls of the œsophagus, extending from its opening at the pharynx to the stomach.

Physiological Anatomy of the Parts concerned in Deglutition.—The parts concerned in this function are the tongue, the muscular walls of the pharynx, and the œsophagus. In the passage of food and drink through the pharynx, it is necessary to completely protect from the entrance of foreign matters a number of openings which are exclusively for the passage of air. These are above, the posterior nares and the Eustachian tubes, and below, the opening of the larynx. The mechanism by which these passages are closed during the acts of deglutition is one of the most interesting subjects connected with this function and has long engaged the attention of physiologists.

The tongue—a muscular organ capable of a great variety of movements, and endowed, as we have seen, with highly important functions connected with mastication—is the chief agent in the first processes of deglutition. Its physiological anatomy has already been considered.

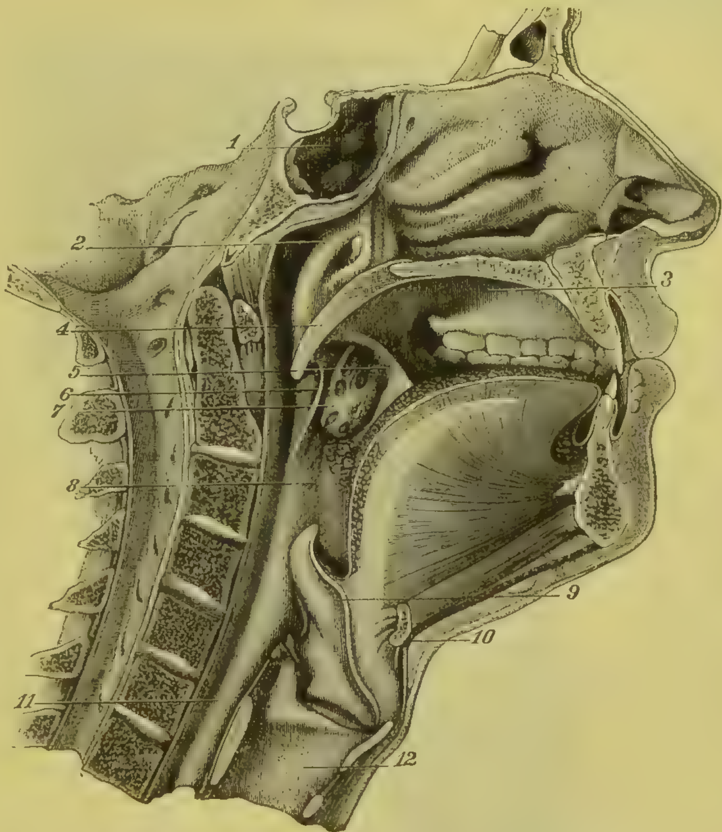


FIG. 52.—*Cavities of the mouth and pharynx, etc.* (Sappey.)

Section in the median line of the face and the superior portion of the neck, designed to show the mouth in its relations to the nasal fossæ, the pharynx, and the larynx: 1, sphenoidal sinuses; 2, internal orifice of the Eustachian tube; 3, palatine arch; 4, velum pendulum palati; 5, anterior pillar of the soft palate; 6, posterior pillar of the soft palate; 7, tonsil; 8, lingual portion of the cavity of the pharynx; 9, epiglottis; 10, section of the hyoid bone; 11, laryngeal portion of the cavity of the pharynx; 12, cavity of the larynx.

The pharynx, in which the most vigorous and complex of the movements of deglutition take place, is an irregular, funnel-shaped cavity, its longest diameter being transverse and opposite the cornua of the hyoid bone, with its smallest portion at the opening into the œsophagus. Its length is about four and a half inches. It is connected superiorly and posteriorly with the basilar process of the occipital bone and the upper cervical vertebræ. It is imperfectly separated from the cavity of the mouth by the velum pendulum palati, a movable musculo-membranous fold continuous with the roof the mouth and marked by a line in the centre, which indicates its original development by two lateral halves. This, which is called the soft palate, when relaxed, presents a concave surface looking toward the mouth, a free, arched border, and a conical process hanging from the centre, called the uvula. On either side of the soft palate, are two curved pillars or arches.

The anterior pillars of the fauces are formed by the palato-glossus muscle on either side and run obliquely downward and forward, the mucous membrane which covers them becoming continuous with the membrane over the base of the tongue. The posterior pillars are more closely approximated to each other than the anterior. They run obliquely downward and backward, their mucous membrane becoming continuous with the membrane covering the sides of the pharynx. Between the lower portion of the anterior and posterior pillars, are the tonsils; and in the substance of, and beneath the mucous membrane of the palate and pharynx, are small glands, which have already been described.

In Fig. 52 are shown the cavities of the mouth and pharynx with their relations to the nares and the larynx.

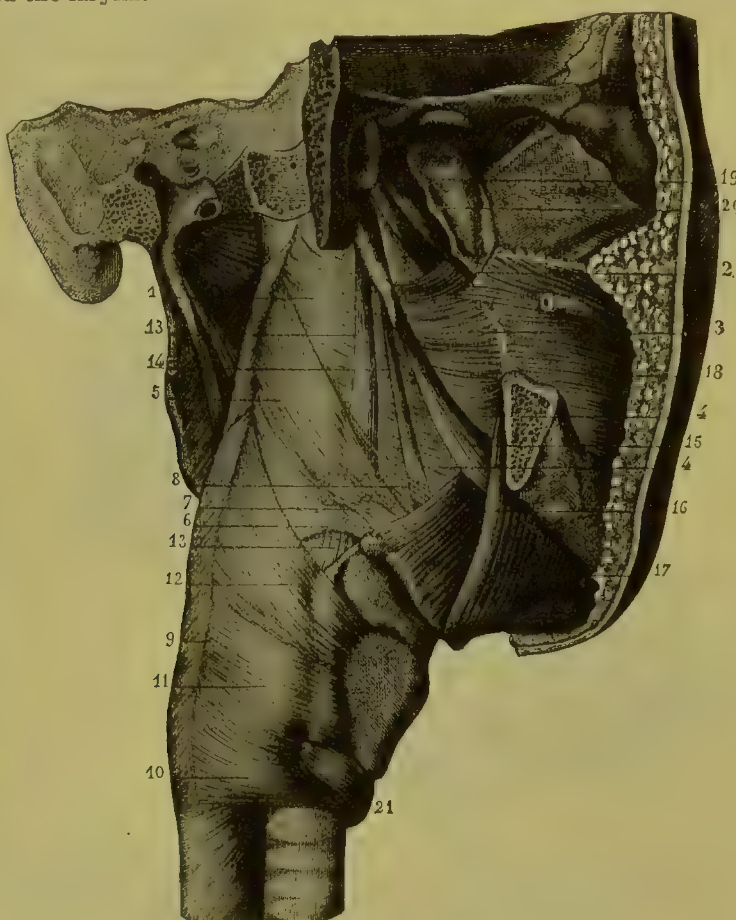


Fig. 58.—*Muscles of the pharynx, etc.* (Sappey.)

1, 2, 3, 4, 4, superior constrictor; 5, 6, 7, 8, middle constrictor; 9, 10, 11, 12, inferior constrictor; 13, 13, stylo-pharyngeus; 14, stylo-hyoid muscle; 15, stylo-glossus; 16, hyo-glossus; 17, mylo-hyoid muscle; 18, buccinator muscle; 19, tensor palati; 20, levator palati.

The isthmus of the fauces, or the strait through which the food passes from the mouth to the pharynx, is bounded above, by the soft palate and the uvula; laterally, by the pillars of the palate and the tonsils; and below, by the base of the tongue.

The openings into the pharynx above are the posterior nares and orifices of the Eustachian tubes. Below, are the openings of the œsophagus and the larynx.

The muscles of the pharynx are the superior constrictor, the stylo-pharyngeus, the middle constrictor, and the inferior constrictor; and it is easy to see, from the situation of these muscles, how, by their successive action from above downward, the food is passed into the œsophagus.

The superior constrictors form the muscular wall of the upper part of the pharynx. Their origin extends from the lower third of the margin of the internal pterygoid plate of the sphenoid bone to the alveolar process of the last molar tooth, the intermediate line of attachment being to tendons and ligaments. The fibres then pass backward and meet in the median raphe, which is attached by aponeurotic fibres to a ridge on the basilar process of the occipital bone, called the pharyngeal spine.

The stylo-pharyngeus muscle has a rounded portion above, by which it arises from the inner surface of the base of the styloid process of the temporal bone. It passes between the superior and middle constrictors of the pharynx, becomes thin, and spreading out, its fibres mingle in part with the fibres of the constrictors and the palato-pharyngeus, and a few pass to be inserted into the upper border of the thyroid cartilage.

Tho middle constrictor is a flattened muscle, arising from the cornua of the hyoid bone and the stylo-hyoid ligament, its fibres passing backward, spreading into a fan-shape, and meeting in the median raphe.

The inferior constrictor is the most powerful of the muscles of the pharynx. It arises by thick, fleshy masses from the sides of the thyroid and cricoid cartilages of the larynx. The inferior fibres curve backward, and the superior fibres, backward and upward, to meet in the median raphe.

The muscles which form the fleshy portions of the soft palate are likewise important in deglutition.

The levator palati, a long muscle of considerable thickness, arises from the apex of the petrous portion of the temporal bone and the adjacent cartilaginous portion of the Eustachian tube; and, spreading out in the posterior portion of the soft palate, as its name implies, it raises the velum.

The tensor palati, sometimes called the circumflexus, is a broad, thin muscle, consisting of a vertical portion, which is fleshy, and a horizontal portion, which is tendinous. The fleshy fibres arise from the scaphoid fossa of the sphenoid bone, pass downward, become tendinous, and wind around the hamular process; after which the muscle spreads out into a thin aponeurosis, which passes to the median line on the anterior portion of the soft palate. Its action is to render the palate tense.

The palato-glossus forms the anterior pillar of the soft palate. It arises from the side of the palate near the uvula and passes to be inserted into the side and dorsum of the tongue. The action of this muscle is to constrict the isthmus of the fauces, by drawing down the soft palate and elevating the base of the tongue.

The palato-pharyngeus forms the posterior pillar of the soft palate. It arises from the soft palate by two fasciculi, and joins with the fibres of the stylo-pharyngeus, to be inserted into the posterior border of the thyroid cartilage. Its action is to approximate the posterior pillars of the palate and depress the velum.

The azygos uvulæ is the small muscle, consisting of two fasciculi, one on either side, which forms the fleshy portion of the uvula. It has no very marked or important action in deglutition.

The mucous membrane of the pharynx, aside from the various glands situated beneath it and in its substance, which have already been described, presents some peculiarities, which are interesting more from an anatomical than a physiological point of view. In the superior portion, which forms a cuboidal cavity just behind the posterior nares, the membrane is darker and much richer in blood-vessels than in other parts. Its surface is smooth and provided with ciliated, columnar epithelium, like that which covers the membrane of the posterior nares. It is marked by a deep antero-posterior groove in the median line; and, on either side, parallel with the median line, are four smaller grooves. In the horizontal portions, the mucous membrane in the central groove adheres to the periosteum of the basilar process, particularly at its posterior extremity. Laterally, below the level of the opening of the Eustachian tubes, and posteriorly, at the point where it becomes vertical, the mucous membrane abruptly changes its character. The epithelial covering is here composed of cells of the pavement-variety, similar to those which cover the mucous membrane of the œsophagus. The membrane is also paler and is less rich in blood-vessels. It is provided with papillæ, some of which are simple, conical elevations, while others present from two to six conical processes with a single base. These papillæ are rather thinly distributed over all of that portion of the mucous surface which is covered with pavement-epithelium.

The contractions of the muscular walls of the pharynx force the alimentary bolus into the œsophagus, a tube possessed of thick, muscular walls, extending to the stomach. The œsophagus is about nine inches in length. It is cylindrical, and rather constricted at its superior and inferior extremities. It commences in the median line behind the lower border of the cricoid cartilage and opposite the fifth cervical vertebra. At first, as it descends, it passes a little to the left of the cervical vertebræ. It then passes from left to right from the fourth or fifth to the ninth dorsal vertebra, to give place to the aorta. It finally passes a little to the left again, and from behind forward, to its opening into the stomach. In its passage through the diaphragm, it is surrounded by muscular fibres, so that when this muscle is contracted in inspiration, its action has a tendency to close the opening.

The coats of the œsophagus are two in number, unless we include, as a third coat, the fibrous tissue which attaches the mucous membrane to the subjacent muscular tissue.

The external coat is composed of an external longitudinal, and an internal circular or transverse layer of muscular fibres. In the superior portion, the longitudinal fibres are arranged in three distinct fasciculi; one in front, which passes downward from the posterior surface of the cricoid cartilage, and one on either side, extending from the inferior constrictors of the pharynx. As the fibres descend, the fasciculi become less distinct and are finally blended into a uniform layer. The circular layer is somewhat thinner than the external layer. Its fibres are transverse near the superior and inferior extremities of the tube and are somewhat oblique in the intermediate portion. The muscular coat is from $\frac{1}{30}$ to $\frac{1}{12}$ of an inch in thickness.

In the upper third of the œsophagus, the muscular fibres are exclusively of the red or striated variety, with some anastomosing bundles; but, lower down, there is a mixture of non-striated fibres, which appear first in the circular layer. These latter fibres become gradually more numerous, until, in the lower fourth, they largely predominate. A few striated fibres, however, are found as low down as the diaphragm.

The mucous membrane of the œsophagus is attached to the muscular tissue by a dense, fibrous layer. It is quite vascular and reddish above, but becomes gradually paler in the inferior portion. The mucous membrane is ordinarily thrown into longitudinal folds, which are obliterated when the tube is distended. Its epithelium is thick, of the pavement-variety, and is continuous with, and similar to the covering of the lower portion of the pharynx. It is provided with papillæ of the same structure as those found in the pharynx, the conical variety predominating. Numerous small, racemose glands are found throughout the tube, forming by their aggregation at the lower extremity, just before it opens into the stomach, a glandular ring.

Mechanism of Deglutition.—For convenience of description, physiologists have generally divided the process of deglutition into three periods. The first period is occupied by the passage of the alimentary bolus backward to the isthmus of the fauces. This may appropriately be considered as a distinct period, because the movements are effected by the action of muscles under the control of the will. The second period is occupied by the passage of the food from the isthmus of the fauces, through the pharynx, into the upper part of the œsophagus. The third period is occupied by the passage of the food through the œsophagus into the stomach.

In the first period, the tongue is the important agent. After mastication has been completed, the mouth is closed and the tongue becomes slightly increased in width, and, with the alimentary bolus behind it, is pressed from before backward against the roof of the mouth. The act of swallowing is always performed with difficulty when the mouth is not completely closed; for the tongue, from its attachments, must follow, to a certain extent, the movements of the lower jaw. The first part of the first period of deglutition, therefore, is simple; but, when the food has passed beyond the hard palate, it comes in contact with the hanging velum, and the muscles are brought into action which render this membrane tense and oppose it in a certain degree to the backward movement of the base of the tongue. This is effected by the action of the tensor-palati and the palato-glossus. The moderate tension of the soft palate admits of its being applied to the smaller morsels, while the opening is dilated somewhat forcibly by masses of greater size.

It is easy to appreciate, in analyzing the first period of deglutition, that liquids and the softer articles of food are assisted in their passage to the isthmus of the fauces by a slight suction force. This is effected by the action of the muscles of the tongue, elevating the sides and depressing the centre of the dorsum, while the soft palate is accurately applied to the base.

The importance of the movements of the tongue during the first period of deglutition is shown by experiments on the inferior animals and by cases of loss of this organ in the human subject. In the experiments of Panizza, which have already been referred to in connection with mastication, it was found that paralysis of the tongue by section of the hypoglossal nerves in dogs deprived the animals of the power of swallowing, even when a bolus of meat or bread was put upon its dorsal surface. In an observation on a young dog, in which we divided both hypoglossal nerves, the effect upon deglutition was very marked. The animal ate with difficulty, the pieces of meat which were given him frequently dropping from the mouth. He was able to swallow only by jerking the head suddenly upward, so as to throw the meat past the base of the tongue; and, even when deglutition commenced, the first steps took place slowly and with apparent difficulty. The process of drinking was very curious. The animal made the usual noise in attempting to drink, but the tongue did not come out of the mouth, and the only way he seemed to get any water was by jerking the head and moving the jaw so as to throw some of the liquid into the mouth. On causing him to drink from a graduated glass, it was found that he drank four fluidounces in four minutes. In the case of a young girl, reported to the Academy of Science, in 1718, by De Jussieu, in which there was congenital absence of the tongue, deglutition was impossible until the food had been pushed with the finger far back into the mouth. In cases of amputation of the tongue, a portion of its base generally remains sufficient to press against the palate and thus act in the first period of deglutition.

The movements in the first period of deglutition are under the control of the will but are generally involuntary. When the food has been sufficiently masticated, it requires an effort to prevent the act of swallowing. In this respect, the movements are like the acts of respiration, except that the imperative necessity of air in the system must, in a short time, overcome any voluntary effort by which respiration has been arrested.

The second period of deglutition involves more complex and important muscular action than the first. By a rapid and almost convulsive series of movements, the food is made to pass through the pharynx into the œsophagus. The movements are then entirely beyond the control of the will, and belong to the kind usually called reflex. After the alimentary mass has passed beyond the isthmus of the fauces, it is easy to observe a sudden and peculiar movement of elevation of the larynx by the action of muscles which usually depress the lower jaw, but which are now acting from this bone as the fixed point. The muscles which produce this movement act chiefly upon the hyoid bone. They are the digastric (particularly the anterior belly), the mylo-hyoid, the genio-hyoid, the stylo-hyoid, and some of the fibres of the genio-glossus. It is probable, also, that the thyro-hyoid acts at this time to draw the larynx toward the hyoid bone. With this elevation of the larynx, there is necessarily an elevation of the anterior and inferior portions of the pharynx, which are, as it were, slipped under the alimentary bolus as it is held by the constrictors of the isthmus of the fauces.

Contraction of the constrictor muscles of the pharynx takes place almost simultaneously with the movement of elevation; and the superior constrictor is so situated as to grasp the morsel of food, and with it the soft palate. The muscles, the constrictors acting from the median raphe, assist to elevate the anterior and inferior walls of the pharynx and pass the food rapidly into the upper part of the œsophagus. All these complex movements are accomplished with great rapidity, and the larynx and pharynx are then immediately returned to their original position.

Protection of the Posterior Nares during the Second Period of Deglutition.—When the act of deglutition is performed with regularity, no portion of the liquids and solids swallowed ever finds its way into the air-passages. The entrance of foreign substances into the posterior nares is prevented in part by the action of the superior constrictors of the pharynx, which, as we have seen, embrace, during their contraction, not only the alimentary mass, but the velum pendulum palati itself, and in part, also, by contraction of the muscles which form the posterior pillars of the soft palate.

During the first part of the second period of deglutition, the soft palate is slightly raised, being pressed upward by the morsel of food. This fact has been observed in cases in which the parts have been exposed by surgical operations, and its mechanism has also been observed in the human subject, by Bidder and Kobelt. In one case—that of a young man who had lost the superior maxillary bone, as well as the zygoma—the soft palate could be observed from its superior surface; and, at each movement of deglutition, the palate, which is naturally inclined downward, became more horizontal, and the posterior wall of the pharynx came forward to meet it. The same movement of the pharynx was observed by Kobelt in the case of a soldier who received a severe sabre-cut in the neck.

While the food is passing through the pharynx, the palato-pharyngeal muscles, which form the posterior pillars of the soft palate, are in a state of contraction by which the edges of the pillars are nearly approximated, forming, with the uvula between them, almost a complete diaphragm between the postero-superior and the antero-inferior parts of the pharynx. This, with the application of the posterior wall of the pharynx to the superior face of the soft palate, completes the protection of the posterior openings of the nasal fossæ. The fact that the posterior pillars are thus contracted and approximated during deglutition may be easily verified by simply watching these parts with a mirror during an effort at swallowing. In a case, observed by Bérard, it was shown that the muscular action of the soft palate was absolutely necessary to the protection of the nares, particularly in swallowing liquids. In this instance, a young lady was affected with complete paralysis of the velum, which allowed liquids to return so freely by the nose in swallowing that she was obliged to retire from observation whenever she drank.

Protection of the Opening of the Larynx, and Uses of the Epiglottis in Deglutition.—The entrance of the smallest quantity of solid or liquid foreign matter into the larynx produces violent and distressing cough. This accident is of not infrequent occurrence, especially when an act of inspiration is inadvertently performed while solids or liquids are in the pharynx. During inspiration, the glottis is opened, and at that time only can a substance of any considerable size find its way into the respiratory passages. Respiration is interrupted, however, during each and every act of deglutition; and there can, therefore, be hardly any tendency at that time to the entrance of foreign substances into the larynx. During a regular act of swallowing, nothing can find its way into the respiratory passages, so complete is the protection of the larynx during the period when the food passes through the pharynx into the œsophagus.

The situation of the epiglottis has naturally led physiologists to attribute to it great importance in preventing the entrance of particles of food and liquids into the larynx. It will be remembered that this cartilaginous, leaf-like process is attached to the anterior portion of the larynx, and is usually erect, lying against the base of the tongue. In the movements of the tongue and larynx incident to deglutition, the epiglottis is necessarily applied to the superior face of the larynx so as to close the opening. Although, during deglutition, the glottis is covered in this way, it is necessary to study closely all the conditions which are involved and to ascertain what is the actual value of each of the various means by which entrance of foreign bodies into the air-passages is prevented, for this protection is accomplished by several distinct provisions.

It is evident, from the anatomy of the parts and the necessary results of the contractions of the muscles of deglutition, that, while the food is passing through the pharynx, the larynx, by its elevation, passes under the tongue as it moves backward, and the soft base of this organ is, as it were, moulded over the glottis. With the parts removed from the human subject or from one of the inferior animals, we can imitate the natural movements of the tongue and larynx, and it is evident that this provision alone must be sufficient to protect the larynx from the entrance of solid or semisolid particles of food, particularly when we remember how the alimentary particles are agglutinated by the saliva and how easy their passage becomes over the membrane coated with a slimy mucus. Experiments on the inferior animals and observations upon the human subject have conclusively settled the question that the deglutition of all articles, except liquids, is generally effected without difficulty when the epiglottis has been removed or lost by accident or disease. The same is true when, in addition, the intrinsic muscles of the larynx have been paralyzed by the section of nerves, or even when closure of the rima glottidis is forcibly prevented. It has been shown, however, by the experiments of Longet, that, when the larynx is in part prevented from performing its movement of ascension, the deglutition of a moist mass of alimentary matter is effected with difficulty and is followed by a sharp cough, indicating the entrance of a certain quantity of foreign matter into the air-passages.

It is impossible for the muscles of the pharynx to contract without drawing together the sides of the larynx, to which they are attached, and assisting to close the glottis. At the same time, as the movements of respiration are arrested during deglutition, the lips of the glottis fall together, as they always do except in inspiration. This fact we have repeatedly observed in demonstrating the respiratory movements of the glottis; for, when the larynx is thus exposed, the animal makes frequent efforts at deglutition. In addition to this passive and incomplete approximation of the vocal chords, it has repeatedly been observed that the lips of the glottis are accurately and firmly closed during each act of deglutition.

Longet justly attaches great importance to the exquisite sensibility of the top of the larynx in preventing the entrance of foreign substances. His experiments of dividing all the nervous filaments distributed to the intrinsic muscles show that their action is not essential. But, on division of the superior laryngeal, the nerve which gives sensibility to the parts, he found that liquids occasionally passed in small quantity into the trachea. This is attributed to the want of sensibility in the mucous membrane above the glottis: "for the animal is not aware in time of the presence of liquid which may accidentally get into the supra-laryngeal cavity, the occlusion of the glottis is sometimes too tardy and does not take place until after the passage of the liquid; or, again, the animal, instead of then making a sudden expiration, makes an unseasonable inspiration which facilitates the introduction of the foreign substance into the air-passages, and the cough does not take place until this is already in contact with the tracheal or bronchial mucous membrane." These experiments strikingly illustrate the conservative function of the acute sensibility of the mucous membrane above the glottis. No foreign substance can find its way into the air-passages by simply dropping into the cavity situated above the vocal cords when respiration is interrupted, but can only enter by being drawn in forcibly and suddenly with an act of inspiration, when the glottis is widely opened. It is now well known to the practical physician that direct applications cannot be made to the interior of the larynx, unless an instrument be suddenly introduced with the inspiratory act; and, at this time, a little dexterity will enable an operator to introduce bodies of considerable size below the vocal chords.

Before the experiments of Magendie, in 1813, physiologists were generally of the opinion, judging from anatomical relations, that the epiglottis had the function of protecting the larynx from the entrance of particles of food during the second period of deglutition. Magendie extirpated the entire epiglottis in dogs and found that the animals swallowed liquids and solids without difficulty, the act being very seldom followed by cough. The observations on deglutition were made an hour after the removal of the epiglottis. In other animals, the superior and inferior laryngeal nerves were divided, thus paralyzing the muscles of the glottis. The deglutition of liquids especially became difficult and was followed generally by cough. As the result of these observations, Magendie came to the conclusion that the larynx is protected during deglutition by closure of the glottis itself.

Although the experiments on animals were apparently conclusive, observations on the human subject have been cited, in which, after destruction of the epiglottis by disease, there existed persistent difficulty in swallowing liquids. As numerous pathological observations of this character have been reported, the question could not be regarded as entirely settled by the researches of Magendie. It was with the view of determining this more rigorously, that farther experiments were instituted in 1841, by Longet.

In investigating this question, Longet removed the epiglottis from six dogs. He found that, in the animals kept until the parts were perfectly cicatrized, more or less cough followed the deglutition of liquids. One of these he kept for six months and found that when he drank milk or water cough never failed to follow. The same fact was noted in three of the animals that were killed on the nineteenth day and in one that was killed on the thirtieth day. In all, the complete excision of the epiglottis was verified by post-mortem examination. In one of the animals, killed two days after the operation, that generally swallowed liquids without coughing, there was found a swelling at the base of the tongue which projected over the larynx.

Several cases of loss of the epiglottis in the human subject are quoted by Longet in support of his view that this part is necessary to the complete protection of the air-passages, particularly in the deglutition of liquids. Two of the most striking of these cases were observed by Larrey, in Egypt. One of these was the case of General Murat, who was wounded by a ball passing through the neck from one angle of the jaw to the other, cutting off the epiglottis, which was expelled by the mouth. In this instance, the difficulty in the deglutition of liquids was so great, that it became necessary to introduce them through a tube passed into the œsophagus. In the other case, the epiglottis was entirely removed by a wound and was preserved and presented to the surgeon. In this instance, the difficulty in the deglutition of liquids was even greater than in the former; each effort at swallowing being followed by convulsive and suffocating cough. This difficulty persisted after the parts had become completely cicatrized. In these cases, it is possible that the injury to muscles and other parts from such severe wounds might interfere with the movements of the larynx or the closure of the glottis and thus disturb deglutition. In a case in which the epiglottis had entirely sloughed away as a consequence of syphilitic disease, observed by Dr. Austin Flint, the difficulty in swallowing liquids, although sufficiently well marked, was by no means so great as in the cases mentioned above. The difficulty in swallowing was noted as not great, but the patient swallowed liquids more easily than solids. The difficulty consisted of cough and loss of breath, as the patient described it. It was less when articles were swallowed while the patient was in the recumbent posture, and food and drink were habitually taken in that position. At the time that this patient, a female, was in the Bellevue Hospital under the observation of Dr. Flint, the deglutition was improving. Dr. Flint noted that, after she had been in the hospital a few days, on causing her to swallow in his presence, the act of deglutition was performed with a certain deliberation but without difficulty. An examination of the parts with the laryngoscope was made by Dr. Church, in the presence of Dr. Flint and Dr. Dalton: "The absence of the epiglottis was determined by sight. The vocal chords were distinctly seen. The little excrescences described as apparent to the touch were visible."

In the case just described, there was not a constant and considerable difficulty in deglutition; but it is stated that difficulty had existed, undoubtedly from the passage of articles into the larynx, and when no such accident took place the act was performed with a "certain deliberation." It is a curious fact, also, that, when the difficulty in swallowing was considerable, deglutition was accomplished most easily in the recumbent posture, in which the tendency of particles of food to pass into the larynx must have been much lessened.

While, with attention on the part of the subject, the larynx may frequently, and perhaps generally, be protected from the entrance of foreign substances during deglutition, after loss of the epiglottis when other parts are not affected, a study of the numerous cases of this lesion as the result of disease or injury shows that the epiglottis is by no means so inefficient in the protection of the larynx as was supposed by Magendie. Still, it is but one of the means which have been provided for this end.

Since the air-passages have been so fully explored by means of the laryngoscope, this instrument has been used to a certain extent in the study of the phenomena of deglutition. In July, 1865, a note was presented to the French Academy of Sciences, giving the results of experiments by Dr. Krishaber on the mechanism of deglutition as studied by autolaryngoscopy, followed by a note on the same subject by M. H. Guinier. Dr. Krishaber, as the result of his observations, gave the following conclusions:

"1st. In the act of deglutition the alimentary bolus passes in one of the pharyngeal grooves, over one of the sides of the epiglottis tilted by the elevation of the larynx; the bolus thus arrives at the œsophagus at the moment when, by the contraction of the constrictor muscles, the pharynx is shortened and brought in front of the mass.

"2d. The deglutition of liquids is effected in the same manner; these passing, however, quite frequently upon the epiglottis itself, which happens very rarely with solid aliments.

"3d. A quantity—extremely small, it is true—of liquid engages itself during normal deglutition around the border of the epiglottis and moistens the mucous membrane of the larynx and even of the vocal chords.

"4th. In gargling, the larynx being widely opened, a larger quantity finds its way into the vocal organ.

"5th. An alimentary bolus may be easily tolerated in the respiratory passages; that is to say, in the larynx, as far as the vocal chords and even in the interior of the trachea.

"6th. The sensibility of the trachea to the impression of foreign bodies is infinitely less than that of the larynx.

"7th. Hard and cold bodies, as, for example, a sound, are not tolerated in the respiratory passages; while any soft body, which can adhere to the mucous membrane and has a temperature like that of the parts touched, is easily tolerated in the respiratory passages and kept in the trachea many minutes without producing the slightest cough."

These observations confirm the views of Longet and others concerning the passage of alimentary substances down the pharynx by the sides of the epiglottis; and, in that case, liquids would almost certainly pass around the borders in quantity sufficient to moisten the mucous membrane below. It must be remembered, however, that the sensibility of the air-passages is very unequal in different persons, and that it may be considerably modified by education of the parts. This should make us hesitate to accept the view that, in gargling, the larynx receives a quantity of liquid, and that an alimentary bolus may be tolerated in the trachea for many minutes without coughing.

To sum up the mechanism by which the opening of the larynx is protected during the deglutition of solids and liquids, we have only to carefully follow the articles as they pass over the inclined plane formed by the back of the tongue and the anterior and inferior part of the pharynx. As the food is making this passage in obedience to the contraction of the muscles which carry the tongue backward, draw up the larynx, and constrict the pharynx, the soft base of the tongue and the upper part of the larynx are applied to each other, with the epiglottis, which is now inclined backward, between them; at the same time the glottis is closed, in part by the action of the constrictor muscles attached to the sides of the thyroid cartilages, and in part by the action of its intrinsic muscles. If the food be tolerably consistent and united into a single bolus, it slips easily from the back of the tongue along the membrane covering the anterior and inferior part of the pharynx; but if it be liquid or of little consistence, a portion takes this course, while another portion passes over the epiglottis, being directed by it into the two grooves or gutters by the side of the larynx. It is by these means, together with those by which the posterior nares are protected, that all solids and liquids are passed into the œsophagus, and the second period of deglutition is safely accomplished.

The third period of deglutition is the most simple of all. It involves merely contractions of the muscular walls of the œsophagus, by which the food is forced into the stomach. The longitudinal fibres shorten the tube and slip the mucous membrane, lubricated by its glairy secretion, above the bolus; while the circular fibres, by a progressive peristaltic contraction from above downward, propel the food into the stomach. The passage of food down the œsophagus was for the first time closely studied by Magendie, who noted, in this connection, many curious and important facts. In numerous experiments on the lower animals, he observed that, while the peristaltic contractions of the upper two-thirds of the tube were immediately followed by a relaxation, which continued till the next act of deglutition, the lower third remained contracted generally for about thirty seconds after the passage of the food into the stomach. During its contraction, this part of the œsophagus was hard, like a cord firmly stretched. This was followed by relaxation; and this alternate contraction and relaxation continued constantly, even when the stomach was empty, although, during digestion, the contractions were frequent in proportion to the quantity of food in the stomach. The contraction was always increased by pressing the stomach and attempting to pass some of its contents into the œsophagus. This provision is undoubtedly important in preventing regurgitation of the contents of the stomach, especially when the organ is exposed to pressure, as in urination or defæcation. We have already noted the action of the crura of the diaphragm, which has a tendency to close the œsophageal opening during inspiration.

The length of time occupied in the third period of deglutition was noted by Magendie in the inferior animals, but we have been unable to find any definite observations on this point in the human subject, although this would have been easy in the cases of gastric fistula which, from time to time, have come under the observation of physiologists. Magendie found that the alimentary bolus sometimes occupied two or three minutes in its passage, and that it was often momentarily arrested in its course. It frequently seems as though we were ourselves conscious of a very slow passage of food down the œsophagus, and not infrequently a piece of bread or a mouthful of liquid is taken to hasten it; but it is not probable that every alimentary bolus remains for two or three minutes in the œsophagus, and liquids undoubtedly are swallowed with considerable rapidity, as they can soon be recognized in the stomach by their temperature. As the lower part of the œsophagus is composed chiefly of unstriped muscular fibres, it is probable that here the contractions are more gradual than in the upper portions.

As we have already had occasion to remark, the muscular movements which take place during all the periods of deglutition are peculiar. The first act is generally involuntary from inattention, but it is under the control of the will. The second act is involuntary, when once commenced, but may be excited by the voluntary passage of solids or liquids beyond the velum pendulum palati. It is impossible to perform the second act of deglutition unless there be some article, either solid or liquid, in the pharynx. It is easy to make three or four successful efforts consecutively, in which there is elevation of the larynx with all the other characteristic movements; but a little attention will show that with each act a small quantity of saliva is swallowed. When the efforts have been frequently repeated, the movements become impossible, until time enough has elapsed between them for the saliva to collect. This fact we personally verified before writing this paragraph, and it was demonstrated to be due to the absence of liquid; for, immediately after, an ounce of water was swallowed without difficulty by sixteen successive movements of deglutition. This experiment also shows the small quantity of liquid (only half a drachm) necessary to excite the contraction of the muscles concerned in the second act.

All the movements of deglutition, except those of the first period, must be regarded as essentially reflex, depending upon an impression made upon the afferent nerves distributed to the mucous membrane of the pharynx and œsophagus.

The position of the body has little to do with the facility with which deglutition is effected. Liquids or solids may be swallowed indifferently in all postures. Bérard states that a juggler, in his presence, passed an entire bottle of wine from the mouth to the stomach, while standing on his head. The same feat we have lately seen accomplished with apparent ease, by a juggler who drank three glasses of beer while standing on his hands in the inverted posture.

Deglutition of Air.—In the celebrated essay of Magendie on the mechanism of vomiting, it is stated that as soon as nausea commenced the stomach began to fill with air, so that, before vomiting occurred, the organ became tripled in size. Magendie showed, farthermore, that the air entered the stomach by the œsophagus, for the distention occurred when the pylorus was ligated. In a subsequent memoir, the question of the deglutition of air, aside from the small quantity which is incorporated with the food during mastication and insalivation, was farther investigated. It was found that some persons had the faculty of swallowing air, and, by practice, Magendie himself was able to acquire it, although it occasioned such distress that it was discontinued. Out of a hundred students of medicine, eight or ten were found able to swallow air.

It is not very uncommon to find persons who have gradually acquired this habit in order to relieve uncomfortable sensations in the stomach; and, when confirmed, it occasions persistent disorder in the process of digestion. Quite a number of cases of this kind are reported by Magendie, and in several it was carried to such an extent as to produce great distention of the abdomen. A curious case of habitual air-swallowing is reported by Dr. Austin Flint, in his work on the Practice of Medicine.

Although the subject of air-swallowing properly belongs to pathology, the fact that the muscles of deglutition are capable, in some individuals, of forcing air into the stomach, is not without physiological interest.

CHAPTER VIII.

STOMACH-DIGESTION.

Physiological anatomy of the stomach—Glandular apparatus in the stomach—Gastric juice—Mode of obtaining the gastric juice—Gastric fistula in the human subject—Secretion of the gastric juice—Composition of the gastric juice—Source of the acidity of the gastric juice—Ordinary saline constituents of the gastric juice—Action of the gastric juice in digestion—Constituents on which the activity of the gastric juice depends—Action of the gastric juice upon meats—Action upon albumen, fibrin, caseine, and gelatine—Action upon vegetable nitrogenized principles—Albuminose, or peptones—Action of the gastric juice upon fats—Action upon saccharine and amylaceous principles—Duration of stomach-digestion—Digestibility of different aliments in the stomach—Action of the gastric juice upon the coats of the stomach—Circumstances which influence stomach-digestion—Character of the contractions of the muscular coat of the stomach—Movements in the cardiac and in the pyloric portion—Mechanism of the movements of the stomach—Rumination, and regurgitation from the stomach—Rumination in the human subject—Vomiting—Condition of the stomach during the act of vomiting—Action of the diaphragm in vomiting—Action of the abdominal muscles in vomiting—Action of the œsophagus in vomiting—Eructation.

Physiological Anatomy of the Stomach.

The most dilated portion of the alimentary canal, in man, is the stomach. It serves the double purpose of a receptacle for the food and an organ in which certain important digestive processes take place. It is situated in the upper part of the abdominal cavity and is held in place by folds of the peritoneum and by the œsophagus. Its form is not easily described. It has been compared to a bagpipe, which it resembles somewhat, when moderately distended. As we should naturally suppose from the fact that the stomach periodically receives considerable quantities of solids and liquids, its form and position are subject to great variations. When empty, it is flattened, and in many parts its opposite walls are in contact. When moderately distended, its length is from thirteen to fifteen inches, its widest diameter, about five inches, and its capacity, one hundred and seventy-five cubic inches, or about five pints. The parts usually noted in anatomical descriptions are: a greater and a lesser curvature; a greater and a lesser pouch; a cardiac, or œsophageal opening; and a pyloric opening, which leads to the intestinal canal. The great pouch is sometimes called the fundus.

The coats of the stomach are three in number; the peritoneal, muscular, and mucous. By some, the fibrous tissue which unites the mucous to the muscular coat is regarded as a distinct covering and is called the fibrous coat.

Peritoneal Coat.—This is simply a process of the peritoneum, similar in structure to the membrane which covers the other abdominal viscera. It is a reflection of the membrane which lines the general abdominal cavity, which, on the viscera, is somewhat thinner than it is on the walls of the cavity. Over the stomach, the peritoneum is from $\frac{1}{300}$ to $\frac{1}{200}$ of an inch in thickness. It belongs to the class of serous membranes and consists of fibres of the white inelastic tissue, mingled with a considerable number of elastic fibres. It is closely adherent to the subjacent muscular coat and is not very abundantly supplied with blood-vessels and nerves. Lymphatics have been demonstrated only in the subserous structure. The surface of the peritoneum is everywhere covered with regularly-polygonal, flattened cells of pavement or tessellated epithelium, closely adherent to each other and presenting a perfectly smooth surface which is continually moistened with a small quantity of watery secretion. An important function of this membrane is to present a smooth surface covering the abdominal parietes and viscera, so as to allow of free movements of the organs over each other and against the walls of the abdomen.

Muscular Coat.—Throughout the whole of the alimentary canal, from the cardiac opening of the stomach to the anus, the muscular fibres forming the middle coat are of the involuntary, pale, or unstriped variety. These fibres, called sometimes muscular fibre-cells, are very pale, with faint outlines, fusiform or spindle-shaped, and contain each an oval, longitudinal nucleus. They are very closely adherent by their sides, and are so arranged as to dovetail into each other, forming sheets of greater or less thickness, depending upon the number of their layers. The muscular coat of the stomach varies in thickness in different animals. In the human subject, it is thickest in the region of the pylorus and is thinnest at the fundus. Its average thickness is about $\frac{1}{24}$ of an inch. In the pylorus, it is from $\frac{1}{16}$ to $\frac{1}{12}$ of an inch thick, and in the fundus, from $\frac{1}{48}$ to $\frac{1}{36}$ of an inch.

The muscular fibres exist in the stomach in two principal layers; an external, longitudinal layer and an internal, circular layer, with a third layer of oblique fibres extending over the great pouch only, which is internal to the circular layer. The direction of the fibres in these layers can generally be seen in a stomach which has been dried and inflated. The longitudinal fibres are continued from the œsophagus and are most marked over the lesser curvature. They are not continued very distinctly over the rest of the stomach. The circular and oblique fibres are best seen when the organ has been everted and the mucous membrane carefully removed. The circular layer is not very distinct to the left of the cardiac opening, over the great pouch, but in other parts it is tolerably regular. Toward the pylorus, the fibres become more numerous, and, at the opening into the duodenum, they form a powerful muscular ring, which is sometimes called the sphincter of the pylorus, or the pyloric muscle. At this point they project considerably into the interior of the organ and cease abruptly at the opening into the duodenum, so as to form a sort of valve, presenting, when contracted, a flat surface looking toward the intestine. The oblique layer takes the place, in great part, of the circular fibres over the great pouch. It extends obliquely over the fundus from left to right and ceases at a distinct line extending from the left margin of the œsophagus to about the junction of the middle with the last third of the great curvature. This anatomical fact is interesting, for it is at about the point where the oblique layer of fibres ceases that the stomach becomes constricted during the movements which are incident to digestion, dividing the organ into two tolerably distinct compartments.

FIG. 54.—*Longitudinal fibres of the stomach.* (Sappey.)

1, lesser curvature; 2, 2, greater curvature; 3, greater pouch; 4, lesser pouch; 5, 6, 6, lower end of the œsophagus; 7, 7, pylorus; 8, 8, longitudinal fibres at the lesser curvature; 9, fibres extending over the greater curvature; 10, 10, a very thin layer of longitudinal fibres over the anterior surface of the stomach; 11, circular fibres seen through the thin layer of longitudinal fibres.

The blood-vessels of the muscular coat are quite numerous and are arranged in a peculiar, rectangular net-work, which they always present in the non-striated muscular tissue. The nerves belong chiefly to the sympathetic system and are demonstrated with difficulty.

FIG. 55.—*Fibres seen with the stomach everted.* (Sappey.)

1, 1, œsophagus; 2, circular fibres at the œsophageal opening; 3, 3, circular fibres at the lesser curvature; 4, 4, circular fibres at the pylorus; 5, 5, 6, 7, 8, oblique fibres; 9, 10, fibres of this layer covering the greater pouch; 11, portion of the stomach from which these fibres have been removed to show the subjacent circular fibres.

Mucous Coat.—Passing from the œsophagus to the stomach, a very marked change takes place in the character of the mucous membrane. The white, hard appearance of the œsophageal lining, due to its covering of pavement-epithelium, abruptly ceases, presenting a sharply-defined, dentated border; and the membrane of the stomach is soft, velvety in appearance, and of a reddish-gray color. In some of the inferior animals, as the horse, the characteristic membrane of the œsophagus is prolonged into the stomach and forms a large, white zone around the cardiac opening, with abruptly-defined edges, contrasting strongly with the rest of the lining membrane of the stomach.

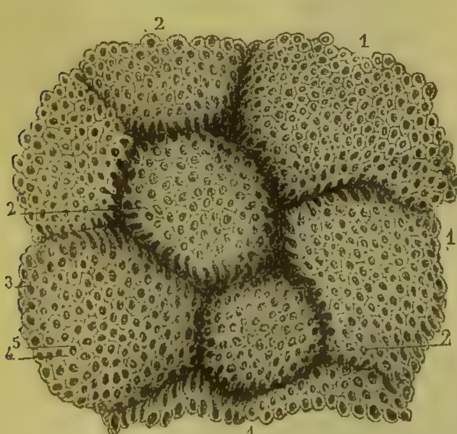


FIG. 56.—*Pits in the mucous membrane of the stomach, and orifices of the glands; magnified 20 diameters.* (Sappey.)

1, 1, 1, 2, 2, 2, 3, pits of different sizes; 4, 5, orifices of the gastric glands.

The mucous lining of the stomach is loosely attached to the submucous muscular tissue and is thrown into large, longitudinal folds, which become effaced as the organ is distended. When the muscular coat of the stomach is in a condition of cadaveric rigidity, the longitudinal folding of the mucous membrane is very marked. If the mucous membrane be stretched or if the stomach be everted and distended, and the mucus, which always exists in greater or less abundance over the surface, be gently removed under a stream of water, the membrane will be found marked with innumerable polygonal pits or depressions, enclosed by ridges, which, in some parts of the organ, are quite regular. These are best seen with the aid of a simple lens, as many of them are quite small. The size of the pits is very variable, but the average is about $\frac{1}{200}$ of an inch. This appearance is not distinct toward the pylorus; the membrane here presenting irregular, conical projections and well-marked villi resembling those found in the small intestine. The surface of the mucous membrane is covered with columnar or prismoidal epithelium, the cells being tolerably regular in shape, each with a clear nucleus and a distinct nucleolus.

The thickness of the mucous membrane of the stomach varies in different parts. It is usually thinnest near the œsophagus and thickest near the pylorus. Its thinnest portion measures from $\frac{1}{72}$ to $\frac{1}{48}$ of an inch; its thickest portion, from $\frac{1}{16}$ to $\frac{1}{12}$ of an inch; and the intermediate portion, about $\frac{1}{24}$ of an inch.

Glandular Apparatus of the Stomach.—Extending from the bottoms of the pits in the mucous membrane of the stomach to the submucous connective tissue, are immense numbers of racemose glands. These are generally arranged in tolerably distinct groups, surrounded by fibrous tissue, each group belonging to one of the polygonal depressions. The tissue which connects the tubes is dense but not abundant. There are marked differences in the anatomy of the glands of the stomach in different parts of the organ, which are particularly interesting, as they are supposed to correspond with differences in the function of various parts of the mucous membrane. There are, indeed, two distinct varieties of glands; the gastric glands, found throughout the organ, except in the pyloric portion, and the mucous glands found chiefly in the pyloric portion, with a few scattered irregularly through the other portions of the mucous membrane. These demand special consideration, as the former are supposed to secrete the gastric juice and are active only during digestion, while the latter secrete a glairy mucus, which is not produced specially during digestion and which has no distinct digestive function with which we are acquainted.

Gastric, or Peptic Glands.—These glands are found throughout the entire extent of the mucous membrane of the stomach, except around the pyloric orifice and in the lesser pouch. In the human subject, their distribution, as compared with that of the mucous glands, is much wider than in most of the inferior animals. They vary in their length with the variations in the thickness of the mucous membrane. Recent researches have shown that all of these glands are racemose. They present, in the upper fourth or fifth of their length, a single tube, lined by a continuation of the columnar epithelium covering the surface of the mucous membrane. Below this, they divide into several branches, primary and secondary, and are lined with rounded cells of glandular epithelium, having the appearance of simple racemose glands. The cells lining the branching tubes are sometimes called peptic cells. They each have a nucleus and a nucleolus, contain numerous granules, and are about $\frac{1}{1200}$ of an inch in diameter. This is the general character of the glands in the greater part of that portion of the mucous membrane which secretes the gastric juice. They readily undergo post-mortem alteration, and, in the human subject, are only to be seen satisfactorily in the fresh stomachs of subjects who have died suddenly, having previously been in a condition of perfect health.

Mucous Glands.—Near the pyloric extremity of the stomach and in the lesser pouch, where the mucous membrane is decidedly paler than over the rest of the organ, the character of the glands is peculiar. As a rule, the glands in these situations are compound; but they do not present more than two or three divisions until they have passed through about one-half of the thickness of the mucous membrane, when they break up into numerous small secondary tubes. The important peculiarity of these glands is that they are lined throughout with columnar epithelium and are everywhere deprived of the cells found in the true peptic glands. The structure of the glands from different portions of the stomach is shown in Fig. 57.

Closed Follicles.—In the substance of the mucous membrane, between the tubes and near their cæcal extremities, are occasionally found closed follicles, like the solitary glands and patches of Peyer of the intestines. These are not always present in the adult, but are generally found in children. They are usually most abundant over the greater curvature, though they may be found in other situations. In their anatomy they are identical with the closed follicles of the intestines and do not demand special consideration in this connection.

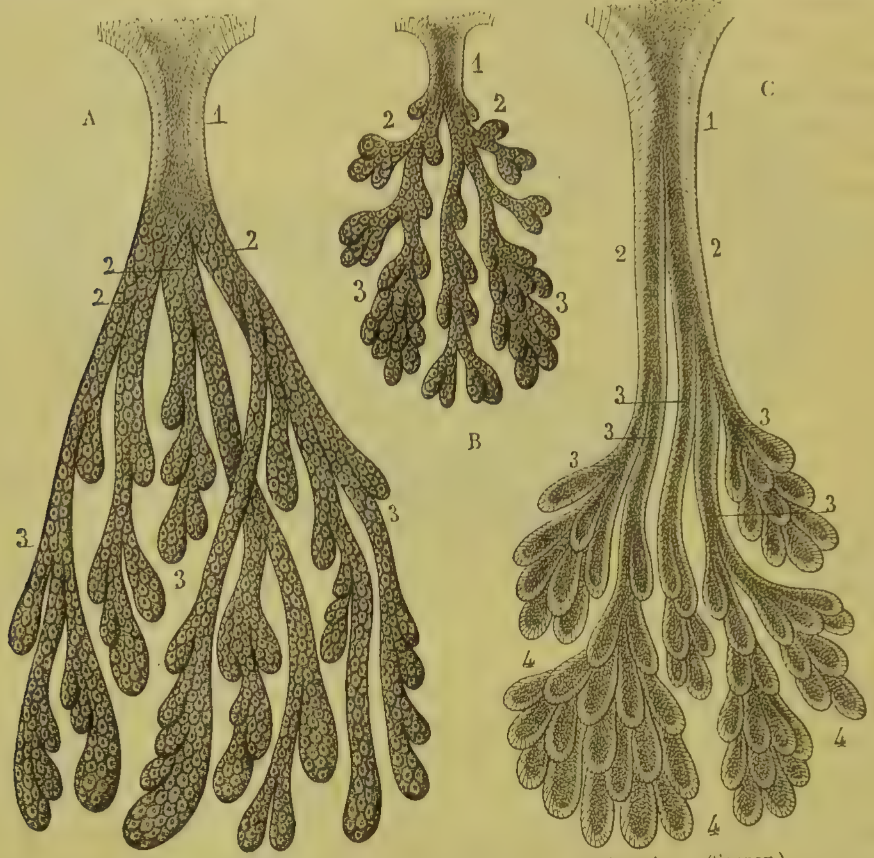


FIG. 57.—*Peptic and mucous glands; magnified* 100 *diameters.* (Sappey.)

A. Peptic gland from the middle portion of the stomach: 1, excretory canal; 2, 2, 2, the three principal branches of the gland; 3, 3, 3, secondary branches filled with rounded cells.
B. Peptic gland from the pyloric portion: 1, excretory canal; 2, 2, the two principal branches: 3, 3, terminal *culs-de-sac.*
C. Mucous gland from the pyloric portion: 1, excretory canal; 2, 2, the two branches; 3, 3, 3, 3, 3, secondary branches; 4, 4, 4, small, terminal, racemose glands.

Gastric Juice.

At the present day it seems profitless to argue the question of the existence of a digestive fluid in the stomach; and the discussions of the earlier physiologists as regards the possibility of the existence of a fluid capable of dissolving the articles of food have only an historical interest. Our definite knowledge of the most important physiological properties of this fluid dates from the celebrated observations of Dr. Beaumont on Alexis St. Martin, the Canadian, who had a large fistulous opening into the stomach. These observations were commenced in May, 1825, and were continued for a number of years. The first publication of them was in the *Philadelphia Medical Recorder*, in 1826.

Mode of obtaining the Gastric Juice.—The ingenious experiments of Dr. Beaumont upon the case of St. Martin gave an impulse to the study of digestion and pointed out the way in which the action of the gastric juice could be investigated. The fact that Dr. Beaumont noted the action of human gastric juice upon all the ordinary articles of food enabled physiologists to compare with it the properties of the secretion obtained from the inferior animals, an indispensable condition in the study of the digestive fluids. In 1843, Blondlot published a treatise on digestion, in which he gave the results of experiments on dogs with fistulous openings into the stomach. This observer is generally spoken of as the first to obtain the gastric juice by the establishment of a fistula into the stomach in the inferior animals; but Longet states that, in December, 1842, Dr. Bassow read a paper before the *Imperial Society of Naturalists of Moscow*, which was published in the Bulletin for that year, in which he gave an account of a number of successful attempts to establish gastric fistulæ in dogs. In the animals operated upon by Bassow, the fistula was not kept open by a canula, and he was much annoyed by its tendency to close. There is no reason to suppose that Blondlot was aware of the experiments of Bassow, which, as Longet remarks, were little known to physiologists and, as far as we are aware, were not quoted in works on physiology before the publication of Longet's treatise, in 1861. With some slight modifications in the operative procedure, the method of Blondlot is the one now in common use.

The establishment of a permanent gastric fistula is now one of the simplest and most common of the physiological experiments. The dog is the animal generally used; and, from the fact that he is not very subject to peritonitis, the operation almost always ends in recovery, and the animal can be trained so that the juice may be obtained in quantity and with great facility. The operative procedure which we have found most convenient is the following:

It is best to choose a dog of medium size, young, but nearly, if not entirely full grown, in perfect health, and of good disposition. Bringing the animal under the influence of ether, he is to be held firmly on the back, and an incision about two inches in length is made in the median line into the abdominal cavity. This incision should be commenced from half an inch to an inch below the ensiform cartilage. Introducing the finger into the abdominal cavity, the stomach can readily be felt, especially if it be moderately distended; and, with a pair of hooked, or bull-dog forceps, that portion of the stomach nearest the wound may be seized and drawn out of the abdomen. It is important to make the fistula into that portion of the anterior wall of the stomach which is nearest the wound, in order to avoid disturbance in the position of the viscera; and the organ is in the most favorable position for the operation if it be moderately distended with food.

A portion of the stomach being drawn out of the abdomen, a slit is made parallel to the longitudinal fibres, just large enough to admit the canula.

A silver canula, about an inch and a quarter in length, half an inch in diameter, and provided with a straight rim or flange at each end about half an inch in width, is now introduced into the stomach and firmly secured in place by a ligature surrounding it and passed in and out through the coats of the stomach near the lips of the wound, like the string of a purse. This canula may be single or, as suggested by Bernard, double, one half screwing into the other so that it may be elongated to twice the length it has when closed. This is somewhat convenient, as the tube may be introduced elongated, and, when the swelling of the parts has subsided, it may be shortened by a key, so as not to project beyond the abdominal walls.

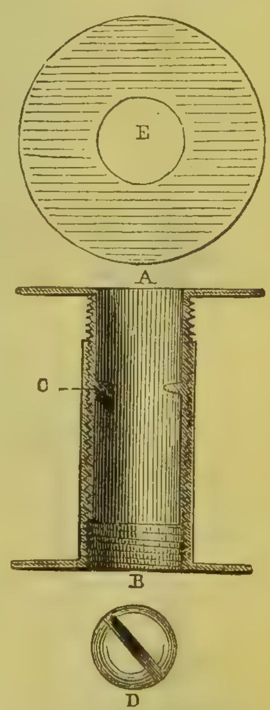


FIG. 58.—*Tube for gastric fistula.* (Bernard.)

A, B, section of the silver tube partly unscrewed; C, projection to receive the key used in turning the screw; D, head of the key; E, extremity of the tube.

After the canula has been firmly fixed in the stomach, the tube, with one of its flanged ends projecting, should be drawn to the upper part of the opening in the abdomen, and the wound closed by sutures passed through the integument, muscles, and peritoneum.

The dog will generally eat on the second or third day after the operation; and peritonitis—aside from the inflammatory action which agglutinates the stomach at the site of the operation to the walls of the abdomen—rarely follows. It is best to feed the animal sparingly a short time before operating, as there is some difficulty in seizing the stomach when it is entirely empty.

Having established a permanent fistula into the stomach, after the wound has cicatrized around the canula, the animal suffers no inconvenience and may serve indefinitely for experiments on the gastric juice. Many physiologists have been in the habit of exciting the flow of this fluid by the introduction into the stomach of pieces of tendon or hard, indigestible articles, on the ground that the fluid taken from the fistula, under these circumstances, is unmixed with the products of stomach-digestion; but it has been shown that the quantity and character of the juice are influenced by the nature of the stimulus which causes its secretion, and it is proper, therefore, to excite the action of the stomach by articles which are relished by the animal. For this purpose, lean meat may be given, cut into pieces so small that they will be swallowed entire, and first thrown into boiling water so that their exterior may become somewhat hardened. The cork is then removed from the tube, which is freed from mucus and *débris*, when the gastric juice will begin to flow, sometimes immediately and sometimes in from three to five minutes after the food has been taken. It flows in clear drops or in a small stream for about fifteen minutes, nearly free from the products of digestion. At the end of this time it is generally accompanied with grumous matter, and the experiment should be concluded if it be desired simply to obtain the pure secretion. In fifteen minutes, from two to three ounces of fluid may be obtained from a good-sized dog, which, when filtered, is perfectly clear; and this operation may be repeated three or four times a week without interfering with the quality of the secretion or injuring the health of the animal.

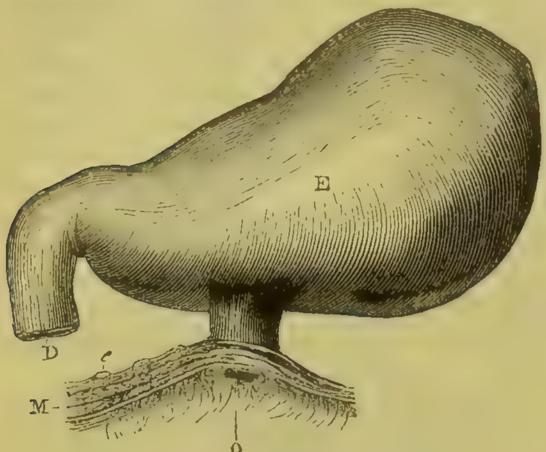


FIG. 59.—*Gastric fistula.* (Bernard.)
E, stomach; D, duodenum; M, muscles of the abdomen, divided; O, opening of the fistula.

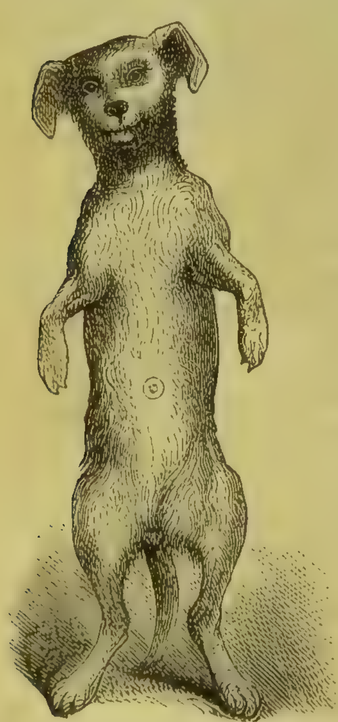


FIG. 60.—*Dog with a gastric fistula.* (Béclard.)

Although instances of gastric fistula in the human subject had been reported before the case of St. Martin and have been observed since that time, the remarkably healthy condition of the subject and the extended experiments of so competent and conscientious an observer as Dr. Beaumont have rendered this case memorable in the history of physiology. It is undoubtedly the fact that this is the only instance on record in which pure, normal gastric juice has been obtained from the human subject; and it served a most important purpose as the standard for comparison of subsequent experiments on the inferior animals. The details of this case, condensed from the monograph of Beaumont, are briefly the following:

Alexis St. Martin, a Canadian *voyageur* in the service of the American Fur Company, eighteen years of age, of good constitution and perfectly healthy, was wounded in the left side by the accidental discharge of a gun loaded with duck-shot. The wound was received on the 6th of June, 1822, and the muzzle of the gun was not more than a yard distant from the body. The contents of the gun entered posteriorly, carrying away integument and muscles from a space the size of the hand, with the anterior half of the sixth rib, fracturing the fifth rib, lacerating the lower portion of the left lobe of the lung and the diaphragm, and perforating the stomach. The patient was seen by Dr. Beaumont twenty-five or thirty minutes after the accident, when the above facts were noted, and an opening into the stomach was discovered large enough to admit the fore-finger. Extensive sloughing took place, and for seventeen days every thing that was swallowed passed out at the wound, and nourishment was administered by the rectum. In the spring of 1824, the wound had cicatrized, and the patient had perfectly recovered his health; but, in the process of cure, seven pieces of cartilage had come away, and three or four inches of the sixth rib, with about half of the lower edge of the fifth rib, had been removed by an operation. The perforation into the stomach was irregularly-circular in form and about two and a half inches in circumference. This opening was closed by a protrusion of the mucous membrane of the stomach in the form of a valve, which could readily be depressed by the finger so as to expose the interior of the organ. This valve effectually prevented the discharge of the contents of the stomach, which had annoyed the patient previous to the winter of 1823–'24.

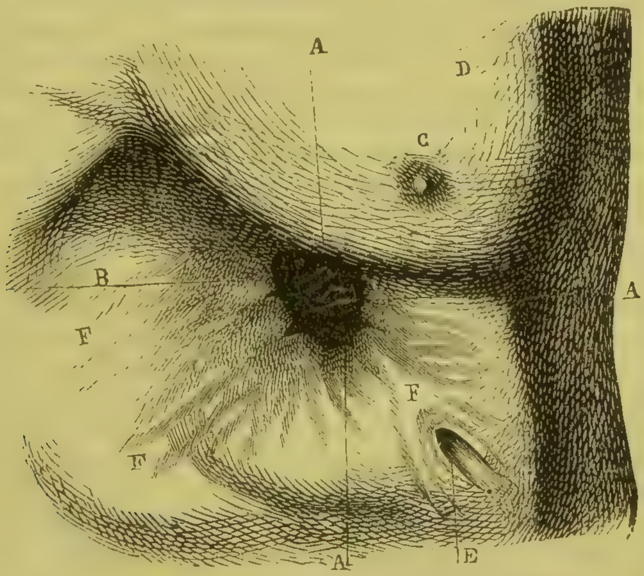


FIG. 61.—*Gastric fistula in the case of St. Martin.* (Beaumont.)
A, A. A. B, borders of the opening into the stomach; C, left nipple; D, chest; E, cicatrices from the wound made for the removal of a piece of cartilage; F, F, F, cicatrices of the original wound.

From May, 1825 until August of the same year, St. Martin was under the observation of Dr. Beaumont and submitted to numerous experiments. At the end of that time, he returned to Canada and was lost sight of for four years, during which time he married and became the father of two children, "worked hard to support his family, and enjoyed robust health and strength." He then came again under the observation of Dr. Beaumont and continued in his service, doing the work of a common servant, until March, 1831. After this he was under observation from time to time until 1836; all this time enjoying perfect health, with good digestion, and having become the father of several more children. The last published observations made upon this case were in 1856.

The following was the method employed by Dr. Beaumont in extracting the juice:

The subject was placed on the right side in the recumbent posture, the valve was depressed within the aperture, and a gum-elastic tube, of the size of a large quill, was passed into the stomach to the extent of five or six inches. On turning him upon the left side until the opening became dependent, the stimulation of the tube caused the secretion to flow, sometimes in drops and sometimes in a small stream. The quantity of fluid ordinarily obtained was from four drachms to an ounce and a half. The usual time for collecting the juice was early in the morning, before he had eaten. It was remarked that under these circumstances there was never an accumulation of gastric juice in the stomach, and its flow was only excited by the stimulus of the tube. It was also repeatedly observed that the introduction of alimentary principles, while the tube was in the stomach, produced an almost instantaneous increase in the flow.

Thanks to these opportunities for observing the action of the human stomach, followed by the experiments of Blondlot and others on the inferior animals, now so common, physiologists have become pretty well acquainted with the phenomena which attend the secretion of the gastric juice.

Secretion of the Gastric Juice.—As the earlier observers were unacquainted with the laws which regulate the production of secreted fluids as distinguished from those which contain only excrementitious principles, their ideas concerning the secretion of the gastric juice were necessarily indefinite. One of the most important facts developed by Beaumont was that the normal solvent fluid of the stomach is only produced in obedience to the stimulus of food, during the natural process of digestion. Recent advances in physiological chemistry have enabled experimenters to correct many errors in the observations of Beaumont concerning the properties and action of the gastric juice, but his descriptions of the phenomena which accompany its secretion have been repeatedly verified.

During the intervals of digestion, the mucous membrane is comparatively pale, "and is constantly covered with a very thin, transparent, viscid mucus, lining the whole interior of the organ." On the application of any irritation, or, better, on the introduction of food, the membrane changes its appearance. It now becomes red and turgid with blood; small pellucid points begin to appear in various parts, which are, in reality, drops of gastric juice; and these gradually increase in size until the fluid trickles down the sides in small streams. The membrane is now invariably of a strongly acid reaction, while at other times it is either neutral or faintly alkaline. The thin, watery fluid thus produced is the true gastric juice. Although the stomach may contain a clear fluid at other times, this is generally abnormal, is but slightly acid, and does not possess the marked solvent properties characteristic of the natural secretion. It has been shown by Beaumont, and his observations have been repeatedly confirmed by experiments on the inferior animals, that the gastric juice is secreted in greatest quantity and possesses the most powerful solvent properties, when food has been introduced into the stomach by the natural process of deglutition. Under these circumstances the stimulation of the mucous membrane is general, and secretion takes place from the entire surface capable of producing the fluid. When any foreign substance, as the gum-elastic tube used in collecting the juice, is introduced, the stimulation is local, and the flow of fluid is comparatively slight. It has been also observed that the quantity immediately secreted on the introduction of food, after a long fast, is always much greater than when food has been taken after the ordinary interval.

While natural food is undoubtedly the proper stimulus for the stomach, and while, in normal digestion, the quantity of gastric juice is perfectly adapted to the work it has to perform, it has been noted that savory and highly-seasoned articles generally produce a more abundant secretion than those which are comparatively insipid. An abundant secretion is likewise excited by some of the vegetable bitters.

Impressions made on the nerves of gustation have a marked influence in exciting the action of the mucous membrane of the stomach. Blondlot found that sugar, introduced into the stomach of a dog by a fistula, produced a flow of juice much less abundant than when the same quantity was taken by the mouth. To convince himself that this did not depend upon the want of admixture with the alkaline saliva, he mixed the sugar with saliva and passed it in by the fistula, when the same difference was observed. It is a curious fact that, in some animals, particularly when they are very hungry, the sight and odor of food will induce secretion of gastric juice.

The gastric juice is probably one of the most sensitive of the secreted fluids to disturbing influences. It was remarked by Beaumont that a febrile condition of the system, the depression resulting from an excess in eating and drinking, or even purely mental conditions, such as anger or fear, vitiated, diminished, and sometimes entirely suppressed secretion by the stomach. At some times the mucous membrane became red and dry, and at others it was pale and moist. In such morbid conditions, it is stated that drinks were immediately absorbed, but that food remained in the stomach undigested for twenty-four or forty-eight hours.

The influence of the nervous system on the secretion of gastric juice, exerted particularly through the pneumogastric nerves, is very marked and important, but its consideration belongs properly to the section on the nervous system.

After the food has been in part liquefied and absorbed and in part reduced to a pultaceous consistence, the secretion of gastric juice ceases; the movements of the stomach having gradually forced that portion of the food which is but partially acted upon in this organ or is digested only in the small intestines, out at the pylorus. The stomach is thus entirely emptied, the mucous membrane becomes pale, its reaction loses its marked acid character and becomes neutral or faintly alkaline.

Secretion in Different Parts of the Stomach.—The differences already noted in the anatomy of the mucous membrane of the stomach in different parts of the organ point to the important question of a possible difference in the physiological action of the secretions of different parts, particularly the pyloric portion and the rest of the general surface. We can learn but little that is definite with regard to this point from observations on the inferior animals, unless they be confirmed in the human subject. The observations, however, of Kölliker, Goll, and Donders, on the pig, are very satisfactory, and subsequently they were fully confirmed as regards the human subject. It is well known that an acidulated infusion of the mucous membrane of the stomach possesses, if properly prepared, all the digestive properties of the true gastric juice, and that this is not the case with similar infusions of the mucous membrane from any other parts. Kölliker, in experiments on artificial digestion made in conjunction with Dr. Goll, "on the gastric mucous membrane of the pig, clearly showed that the two kinds of glands entirely differ in respect of their solvent power; inasmuch as those with the round cells dissolved acidulated coagulated protein-compounds in a very short time; those with cylindrical epithelium, on the contrary, either did not operate at all, or produced a slight effect only after a longer period." The same author farther states that these observations were confirmed by Donders and himself in the human stomach.

Although the character of the secretion in different parts of the stomach is not the same in all animals, it must be admitted that, in man, the mucous membrane of the stomach, in what is called the pyloric zone, does not secrete the true, acid, solvent, gastric juice. In other words, this fluid is produced only in those portions of the stomach in which the mucous membrane is provided with tubes lined with cells of glandular epithelium, or what have been called the stomach-cells.

In most of the modern works on physiology, allusion is made to the probable quantity of gastric juice secreted in the twenty-four hours. The estimates on this point can be only approximative, even in the inferior animals, and they give no definite information concerning the normal quantity in the human subject. Bidder and Schmidt, Lehmann, Corvisart, and others, have made calculations of the probable quantity, either by collecting the juice for a certain time and multiplying the quantity thus obtained by a number to represent the whole twenty-four hours, or by ascertaining the amount of fluid required to digest a certain weight of food and estimating from this the quantity necessary to dispose of all the food taken during the day. Both of these methods are manifestly incorrect. In the first, the intermittency of the secretion is not taken into account; and, in the second, it is incorrectly assumed that digestion out of the body is accomplished precisely as it takes place in the stomach.

Dr. Beaumont was sometimes able to collect, in from ten to fifteen minutes, two ounces of pure gastric juice, simply by the stimulation produced by the gum-elastic catheter used in the operation; but he expressly states that, in this case, only a part of the mucous membrane is excited to secretion, while the flow is very much increased by the introduction of food by the mouth, which produces a general excitation of the secreting membrane. Estimates like those of Bidder and Schmidt, which put the quantity of gastric juice secreted in twenty-four hours by a healthy man of ordinary size at six thousand four hundred grammes, or about fourteen pounds, are probably not exaggerated, although they are of necessity merely approximative.

The enormous quantity of fluid daily secreted by the mucous membrane of the stomach would excite surprise were it not considered that, after this fluid has performed its office in digestion, it is immediately reabsorbed, and but a small quantity of the secretion exists in the stomach at any one time. During digestion, a circulation of material is going on, in which the stomach is continually producing, out of materials furnished by the blood, a fluid which liquefies certain elements of the food and, as fast as this is accomplished, is absorbed again by the blood, together with the principles that have been thus digested.

Composition of the Gastric Juice.

The gastric juice is mixed in the stomach with more or less mucus secreted by the lining membrane. When drawn by a fistula, it generally contains particles of food, which have become triturated and partially disintegrated in the mouth, and is always mixed with a certain quantity of saliva, which is swallowed during the intervals of digestion as well as when the stomach is in a state of functional activity. By adopting certain precautions, however, the fluid may be obtained nearly free from impurities, except the admixture of saliva. The juice taken from the stomach during the first moments of its secretion and separated from mucus and foreign matters by filtration is a clear fluid, of a faint yellowish or amber tint, and possessing little or no viscidity. Its reaction is always strongly acid; and it is now a well-established fact that any fluid, secreted by the mucous membrane of the stomach, which is either alkaline or neutral, is not the normal gastric juice.

The specific gravity of the gastric juice in the case of St. Martin, according to the observations of Beaumont and Silliman, was 1005; but later, Dr. F. G. Smith found it in one instance, 1008, and in another, 1009. There is every reason to suppose that the fluid, in the case of St. Martin, was perfectly normal, and from 1005 to 1009 may be taken as the range of the specific gravity of the gastric juice in the human subject. There is undoubtedly considerable variation, as regards specific gravity, in the inferior animals.

The gastric juice is described by Beaumont as inodorous, when taken directly from the stomach; but it has rather an aromatic and a not disagreeable odor when it has been kept for some time. It is a little saltish, and its taste is similar to that of "thin, mucilaginous water slightly acidulated with muriatic acid." The gastric juice from the dog has something of the odor peculiar to this animal.

It has been found by Beaumont, in the human subject, and by those who have experimented on the gastric juice of the lower animals, that this fluid, if kept in a well-stoppered bottle, will retain its chemical and physiological properties for an indefinite period. The only change which it undergoes is the formation of a pellicle, consisting of a vegetable, confervoid growth, upon the surface, some of which breaks up and falls to the bottom of the vessel, forming a whitish, flocculent sediment. We have now (1875) a specimen of gastric juice which was taken from a dog with a gastric fistula in January, 1862. It has no putrefactive odor and is apparently in the same condition as when it was first drawn. In addition to this remarkable faculty of resisting putrefaction, this process is arrested in decomposing animal substances, both when taken into the stomach and when exposed to the action of the gastric juice out of the body.

There are on record no minute quantitative analyses of the human gastric juice, except those by Schmidt, of the fluid from the stomach of a woman with gastric fistula; and in this case there is reason to suppose that the secretion was not normal. The analysis of the gastric juice of St. Martin by Berzelius was not minute. The analyses of Schmidt give less than six parts per thousand of solid matter, while Berzelius found over twelve parts per thousand. In all the comparatively recent analyses, there have been found a free acid or acids; a peculiar organic matter, generally called pepsin; and various inorganic salts, among which may be mentioned as most important, the chlorides of sodium, potassium, and calcium, with the phosphates of lime, magnesia, and iron. Of these constituents, the salts possess little physiological importance as compared with the organic matter and the acid principles.

The following analysis by Bidder and Schmidt gives the mean of nine observations upon dogs:

Table of Solid Constituents of the Gastric Juice of the Dog.
(Bidder and Schmidt.)

Ferment (pepsin.)	17·127
Free hydrochloric acid (?)	3·050
Chloride of potassium	1·125
Chloride of sodium	2·507
Chloride of calcium	0·624
Chloride of ammonium	0·468
Phosphate of lime	1·729
Phosphate of magnesia	0·226
Phosphate of iron	0·082
	26·938

In another series of three experiments, in which the saliva was allowed to pass into the stomach, the proportion of free acid was 2·337, and the proportion of organic matter was somewhat increased.

Organic Principle of the Gastric Juice.—This principle, called pepsin or gasterase, is an organic nitrogenized body, peculiar to the gastric juice, and, as we shall see farther on, is essential to its digestive properties. When the gastric fluid was first obtained, even by the imperfect methods employed anterior to the observations of Beaumont and of Blondlot, an organic matter was spoken of as one of its constituents.

Experiments on artificial digestive fluids, by Eberle, Schwann and Müller, Wasmann, and others, have demonstrated that acidulated infusions of the mucous membrane of the stomach, possessing all the physiological properties of the gastric juice, contain an organic matter, first isolated by Wasmann, on which the solvent powers of these acid fluids seem to depend. Mialhe, who has obtained this substance in great purity by the process recommended by Vogel, describes the following properties as characteristic of the organic matter in artificial gastric juice: Dried in thin slices on a plate of glass, it is in the form of small, grayish, translucent scales, with a faint and peculiar odor and a feebly bitter and nauseous taste. It is soluble in water and in a weak alcoholic mixture, but is insoluble in absolute alcohol. A solution of it is rendered somewhat turbid by a temperature of 212° Fahr., but it is not coagulated, although it loses its specific properties. It is not affected by acids but is precipitated by tannin, creosote, and a great number of the metallic salts. This substance dissolved in water slightly acidulated possesses, in a very marked degree, the peculiar solvent properties of the gastric juice; but it has been found by Payen and Mialhe not to be so active as the principle extracted from the gastric juice itself, which is described by Payen under the name of gasterase. In the abattoirs of Paris, Mialhe collected from the secreting stomachs of calves as they were killed, from six to ten pints of gastric juice; and from this he extracted the pure pepsin by the process recommended by Payen, which consists merely in one or two precipitations by alcohol. This substance he found to be identical with the principle obtained by Payen from the gastric juice of the dog. Its action upon albuminoid matters was precisely the same as that of pepsin extracted from artificial gastric juice, except that it was more powerful.

Source of the Acidity of the Gastric Juice.—Réaumur and Spallanzani recognized that the fluid from the stomach has, at certain times, an acid reaction; and subsequent observations have confirmed this fact and have shown that this reaction is invariable during digestion. But, although the most distinguished and skilful chemists of the day have attempted to ascertain the source of this acidity, from Prout, in 1823, to Blondlot, in 1858, embracing Leuret and Lassaigne, Tiedemann and Gmelin, Berzelius, Chevreul, Bidder and Schmidt, Dumas, Lehmann, Bernard and Barreswil, with a host of others, the question has not yet received a solution which is generally accepted.

The method made use of by some of those who profess to have found free hydrochloric acid in the gastric juice has been to subject the fluid to distillation, testing the acid fluid which passes over with nitrate of silver; but the experiments of Bernard and Barreswil on the gastric juice from dogs, and the more recent observations of Dr. F. G. Smith on the gastric juice from St. Martin, have shown that this process is really of little value. The following observations by Bernard and Barreswil seem to show that, although hydrochloric acid may be obtained from gastric juice by distillation, it does not necessarily exist in the fluid in a free state; which is a very important consideration in a question in which every thing depends upon the absolute accuracy of modes of analyses:

In subjecting the gastric juice of the dog to distillation at a low temperature, with all the necessary precautions, it was found that the first products did not present an acid reaction. It was at first thought that this would be a ground for the exclusion of hydrochloric acid, which is considered to be volatile; but it was found that, in the distillation of water which had been slightly acidulated with hydrochloric acid, the first products were neutral, and the acid was disengaged only in the fluid which passed over toward the last periods of the process. On again distilling the gastric juice, it was found that the product was neutral, presenting no precipitate with the nitrate of silver, until about four-fifths of the fluid had passed over; that afterward, the fluid which passed over was distinctly acid, but did not precipitate with the salts of silver; and "finally, only toward the last instants, when there remained only a few drops of gastric juice to evaporate, the acid liquid which was produced gave a marked precipitate with the salts of silver, which was not dissolved by concentrated nitric acid." It was found that the addition to the gastric juice of a small quantity of oxalic acid produced a marked opacity due to the formation of the insoluble oxalate of lime, while an equal quantity of the same reagent produced no opacity in water containing a proportion of two thousandths of hydrochloric acid, to which chloride of calcium had been added. From this experiment, Bernard concluded that the hydrochloric acid in the gastric juice exists in the condition of a chloride and not in a free state.

Prof. F. G. Smith, who had an opportunity of examining the gastric juice from St. Martin, in 1856, took the fluid from the stomach after two ounces of dry bread had been chewed and swallowed, and subjected it to distillation. The first fluid which passed over was neutral, and the residue, after the temperature had been somewhat raised, produced a slight precipitate with the nitrate of silver, which was soluble in ammonia. In another experiment, a mixture of lactic acid and chloride of sodium in solution was subjected to distillation, and the product formed a slight precipitate with the nitrate of silver, which was soluble in ammonia. In another experiment, a mixture of lactic acid and chloride of sodium in solution was subjected to distillation, and the product formed a slight precipitate with the nitrate of silver. The precipitation, in this instance, was attributed to the passage of a small quantity of chloride of sodium with the vapors, and it is to this, also, that he attributes the opalescence of the products of distillation of the gastric juice, when treated with the nitrate of silver. These experiments are of great interest in so far as they confirm the observations of Bernard, Villefranche, and Barreswil, on the gastric juice of the dog.

The experiments of Lehmann are even more conclusive. He found that pure gastric juice, when evaporated *in vacuo*, develops hydrochloric acid; but he also found that chloride of calcium is decomposed during evaporation with lactic acid *in vacuo* and attributes the generation of hydrochloric acid in the gastric juice to the decomposition with this salt, and not the chloride of sodium, as was thought by Bernard, Villefranche, and Barreswil.

The addition of a small quantity of oxalic acid to gastric juice produces a precipitate of the insoluble oxalate of lime, which does not take place in the presence of free hydrochloric acid, even when it exists in very minute quantity. No one has denied that this reaction always takes place in the gastric juice; but, in this fluid, is it inconsistent with the presence of a small quantity of hydrochloric acid? We have found that the addition of two drops of ordinary hydrochloric acid to half a fluidounce of gastric juice does not prevent the precipitation of the oxalate of lime, which, in the single observation referred to, was prevented only when the quantity of acid was increased to five drops. On adding oxalic acid to fresh urine, the precipitate of oxalate of lime was marked; but, after the addition of two drops of ordinary hydrochloric acid, this reaction did not take place. Taken in connection with the fact that many of the ordinary chemical reactions are prevented or modified in fluids containing organic substances, this would lead us to inquire whether free hydrochloric acid may not exist in small quantity in the gastric juice, and, as an exceptional phenomenon, the reaction between the oxalic acid and the soluble salts of lime still take place, or whether the acid may not unite with the organic principle, forming, as was suggested by Schiff, chlorohydropeptic acid. In support of this latter view, it is to be remembered that Mulder has formed combinations of organic principles with various of the mineral acids, such as the sulphuric and the hydrochloric. In these compounds, the acid character remains, but the ordinary reactions of the acid are lost.

With the abundant opportunities which have been presented for the chemical study of the gastric juice, not only in the inferior animals but in man, and in view of the numerous elaborate researches into the nature of this fluid by the most skilful physiological chemists of the day, it is a matter of surprise that the question of the existence of free hydrochloric acid, or its condition as regards combination with the organic matter, is not settled. It certainly cannot now be regarded as determined beyond question. If, as is supposed by Bidder and Schmidt, there be a proportion of chlorine which cannot be accounted for by the quantity of ordinary bases in the gastric juice, it probably does not exist as free hydrochloric acid, but it is in some way united with organic matter.

In 1786, Macquart indicated the presence of lactic acid in the gastric juice of the calf, attributing the acidity of the gastric juice of the ox and the sheep to free phosphoric acid. Since then there have been numerous analyses in which this principle has been said to be found. Among those who early adopted this view, may be mentioned Chevreul, Graves, and Leuret and Lassaigne. After the analyses by Prout, in 1823, and the observations of Beaumont on the fluid obtained from St. Martin, and until the publication of the experiments of Bernard, Villefranche, and Barreswil, in 1844, hydrochloric acid was generally supposed to be the free acid of the gastric juice. It is chiefly on the last-named observations—which have been supported by Bernard in his later publications and by the confirmatory experiments of Lehmann and others—that those who admit the presence of free lactic acid in quantity in the gastric juice rest their belief.

We have already referred to the experiments of Bernard, which show that an artificial fluid containing chloride of sodium and lactic acid in solution behaves, during distillation, in every way like the normal gastric juice. These show, also, how hydrochloric acid may be produced during the last period of the distillation by decomposition of the chlorides. We have seen that this observation was confirmed by Lehmann, who noted the same reaction during evaporation at the ordinary temperature, *in vacuo*, although he supposed the action in the gastric juice to be upon the chloride of calcium instead of the chloride of sodium. Lehmann found in the acid residue, free lactic acid, lactate of lime, and alkaline chlorides. Bernard and Lehmann have brought forward other experimental facts to show that the gastric juice contains lactic acid. If starch be boiled in a solution containing hydrochloric acid, it soon loses its property of forming a blue compound with iodine; while if it be boiled with lactic acid, no such change is observed. If starch be boiled with a solution containing hydrochloric acid, to which has been added a soluble lactate in excess, it remains unaltered; which shows, according to Bernard, that hydrochloric acid in a free state cannot exist in the presence of an excess of a salt of lactic acid. By similar experiments, the same observer assumes to prove that the existence of hydrochloric acid is inadmissible in the presence of a phosphate or an acetate in excess. Lehmann has found that starch boiled with gastric juice retains the property of being colored blue by iodine. These experiments are considered by Bernard as positive proof that the acid of the gastric juice is the lactic; and the fact "seems to him to be at the present day beyond contestation." The facts adduced by Lehmann, however, are even stronger. By operating upon a large quantity of gastric juice, he formed the lactates in such a quantity that he was enabled to subject them to ultimate analysis and determine positively the nature of the acid. He found that the acid had the composition of lactic acid formed from sugar, and not that of the acid formed from the juice of the muscular tissue.

In view of the facts above mentioned and the somewhat uncertain basis on which the supposition of the presence of free hydrochloric acid is founded, it seems almost certain that the principal free acid of the gastric juice is the lactic. It is important to remember that, while the experiments of Bernard and Lehmann were made on gastric juice from the dog, they have been confirmed, in their essential particulars, by the more recent observations of Prof. F. G. Smith on the normal gastric juice from the human subject.

It now only remains to discuss the question of the existence in the gastric juice of the acid phosphate of lime, to the exclusion altogether of free acids; a theory first proposed by Blondlot in 1843, and entertained and defended by him, as late as 1858, notwithstanding the fact that this view has met with no favor among physiologists.

To Blondlot belongs the rare merit of having been one of the first, if not the very first, to propose and execute an experiment by which the normal gastric juice could be obtained in quantity from a living animal. In his first analysis of the fluid thus obtained, he denied the existence of any acid principles except the biphosphate of lime. This view he holds at the present day; and, notwithstanding the elaborate researches of the most distinguished physiological chemists, in all of which a free acid of some kind has been recognized, he still ardently defends his original position. The question of the existence in the gastric juice of the acid phosphate of lime, to the exclusion of free acids, may be discussed in a few words.

Assuming that the gastric juice contains a free acid, a view which the arguments of Blondlot fail to disprove, the question arises whether the biphosphate of lime may not also exist in this fluid. On this point there can be no doubt. All the modern analyses of the gastric juice give the phosphate of lime as one of its constituents; and Blondlot justly remarks that it is strange to see, in certain analyses, the neutral phosphate of lime and hydrochloric or lactic acid put down as existing together, as though the phosphoric acid were able to retain the two equivalents of the base in the presence of either of these two acids. The fact is, that basic phosphate of lime, a salt insoluble in pure water but soluble in acid solutions, is invariably decomposed in the presence of acids as powerful as the hydrochloric or the lactic. It then loses two equivalents of the base and is transformed into an acid phosphate.

There can be no doubt of the constant presence of the acid phosphate of lime in the gastric juice, at least in the dog, and its quantity is undoubtedly increased in this animal during the digestion of bones, by the action of the acid fluid upon their phosphatic constituents; but the arguments of Blondlot against the existence of a free acid have little or no weight. One of those on which most stress is laid is that the gastric juice does not act upon the carbonates, which would undoubtedly be the case if it contained a free acid. The simple reply to this is that there is sufficient evidence to show that it is not the fact. Melsens, using a specimen of fluid obtained by Blondlot from the dog and given to Dumas, found that seventy-three grammes of juice dissolved, in twenty-four hours, 0·108 of a gramme of calcareous spar (crystallized carbonate of lime). He confirmed this observation by several experiments, so that there can be no doubt as to its accuracy.

It is plain, therefore, that, while the acid phosphate of lime has been shown to be a constant constituent of the pure gastric juice, contributing, in a certain degree, to its acidity, it is not by any means to be regarded as the sole acid principle; the phosphate probably existing in this form by virtue of the presence in this fluid of a free acid.

On what does the acidity of the gastric juice depend? This is the simple question to which the foregoing discussion naturally leads; and it is one which can be answered almost with positiveness, although it is not settled to the satisfaction of all physiologists and there are some conflicting observations which can be harmonized only by new researches.

Aside from the conditions under which acids, such as butyric, acetic, or lactic, are developed from articles of food taken into the stomach, the evidence is strongly in favor of free lactic acid as the principle on which the gastric juice mainly and constantly depends for its acidity. There also exists a certain quantity of biphosphate of lime; and this is the only condition in which a phosphate of lime can exist in the presence of free lactic acid.

The observations of Bidder and Schmidt indicate, apparently, a quantity of chlorine in the gastric juice not to be accounted for by the proportion of bases obtained by ultimate analysis. There is evidence sufficiently positive to show that there is no hydrochloric acid in the gastric juice, in a condition which allows the fluid to present the reactions which are observed when this acid exists in a free state. If there be any hydrochloric acid not in combination with metallic bases, it is united with organic matter in such a way as to prevent the manifestations of its ordinary properties, except that of acidity. The fact that some of the mineral acids can be made to unite in this way with albuminoid substances lends color to this supposition; although farther investigations are necessary to demonstrate that this takes place in the gastric juice.

Ordinary Saline Constituents of the Gastric Juice.—It has been experimentally demonstrated that artificial fluids, containing the organic principle of the gastric juice and the proper proportion of free acid, are endowed with all the digestive properties of the normal secretion from the stomach, and that these properties are rather impaired when an excess of its normal saline constituents is added or when the relation of the salts to the water is disturbed by concentration. Boudault and Corvisart evaporated two hundred grammes of the gastric juice of the dog to dryness and added to the residue fifty grammes of water. They found that the fluid thus prepared, containing four times the normal proportion of saline principles, did not possess by any means the energy of action on alimentary substances of the normal secretion. These facts have led physiologists to attach little importance to the ordinary saline principles found in the gastric juice.

In the various analyses of the pure juice from the human subject and the inferior animals, particularly dogs, chemists have discovered the chlorides of sodium, calcium, potassium, and ammonium, the phosphate of lime (necessarily in the form of the biphosphate), magnesia, and a small proportion of phosphate of iron. Of these principles, the chloride of sodium has always been found to exist in greatest abundance.

Action of the Gastric Juice in Digestion.

In treating of the composition of the gastric juice, frequent allusion has been made to its solvent action in digestion and to the constituents on which this property depends. Certain of the principles most readily attacked by this fluid are acted upon by weak acid solutions containing no organic matter; but, although some physiologists have been disposed to regard the processes of solution which take place in the stomach as dependent merely on the presence of a free acid, it is now well established that the presence of a peculiar organic principle is an indispensable condition to the performance of real digestion by the gastric fluid. It has also been fully established that fluids containing the organic principle of the gastric juice have no digestive properties unless they also possess the proper degree of acidity; and it is as well settled that fluids containing acids alone have no action on albuminoids similar to that which takes place in digestion, and that when these principles are dissolved by them it is simply accidental.

It is a curious fact that the presence of any one particular acid does not seem essential to the digestive properties of the gastric juice, so long as the proper degree of acidity is preserved. In the experiments of Bernard, Villefranche, and Barreswil, after saturating the gastric juice with neutral phosphate of lime and adding acetic, phosphoric, or hydrochloric acid in such quantity that it certainly existed in a free state, the digestive properties of the fluid were retained. These authors regard it as essential that the normal acid of the gastric juice should be thus capable of being replaced indifferently by other acids; for, they say, in case any salt were introduced into the stomach which would be decomposed by the lactic acid of the gastric juice, digestion would be interfered with, unless the liberated acid could take its place. It can readily be appreciated that transient disturbances might occur from this cause, were the existence of any one acid principle indispensable to the digestive properties of the gastric juice; while, if only a certain degree of acidity were required, this condition might be produced by any acid, either derived from the food or secreted by the stomach.

Enough has already been said, under the head of the organic principle of the gastric juice, to show that the presence of this substance is likewise a condition indispensable to digestion.

As far as has been ascertained by experiments upon artificial digestion, the mucus, which always exists in greater or less quantity in the stomach, does not seem to be important. It is usual in these experiments to separate mucus and extraneous matters from gastric juice by filtration before it is used; and the digestive properties of the fluid thus treated are not sensibly affected when the mucus is allowed to remain.

In studying the physiological action of the gastric juice, it must always be borne in mind that the general process of digestion is accomplished by the combined, as well as the successive action of the different digestive fluids. The act should be viewed in its *ensemble*, rather than as a process consisting of several successive and distinct operations, in which different classes of principles are dissolved by distinct fluids. The food meets with the gastric juice, after having become impregnated with a large quantity of saliva; and it passes from the stomach to be acted upon by the intestinal fluids, having imbibed both saliva and gastric juice. By studying the different digestive fluids in too exclusive a manner, many physiologists, while professing to assign definite and distinct properties to each, thus investing the function of digestion with the attraction of simplicity, have necessarily ignored or distorted facts and have assumed a completeness for the sum of our information on this subject, which does not exist.

When the acts which take place in the mouth are properly performed, the following alimentary substances, comminuted by the action of the teeth and thoroughly insalivated, are taken into the stomach: muscular tissue, containing the muscular substance enveloped in its sarcolemma, blood-vessels, nerves, white fibrous tissue holding the muscular fibres together, interstitial fat, and a small quantity of albumen, fibrin, and corpuscles from the blood, all combined with a considerable quantity of inorganic saline matters; albumen, sometimes unchanged, but generally in a more or less perfectly coagulated condition; fatty matter, sometimes in the form of oil and sometimes enclosed in vesicles, constituting adipose tissue; gelatine and animal matters in a liquid form extracted from meats, as in soups; caseine, in its liquid form united with butter and salts in milk, and coagulated in connection with various other principles in cheese; vegetable nitrogenized principles, of which gluten may be taken as the type; vegetable fats and oils; saccharine principles, both from the animal and the vegetable kingdom, but chiefly from vegetables; the different varieties of amylaceous principles; and, finally, organic acids and salts, derived chiefly from vegetables. These principles, particularly those from the vegetable kingdom, are united with more or less innutritious matter, such as cellulose. They are also seasoned with aromatic principles, condiments, etc., which are not directly used in nutrition.

The various articles coming under the head of drinks are taken without any considerable admixture with the saliva. They embrace water, the various nutritious or stimulant infusions (including alcoholic beverages), with a small proportion of inorganic salts in solution.

All the articles enumerated above are more or less modified in the stomach; and the action of the gastric juice upon them will now be taken up in detail.

Action of the Gastric Juice upon Meats.—There are three ways in which the action of the gastric juice upon the various articles of food may be studied. One is to subject them to the action of the pure fluid taken from the stomach, as was done by Beaumont, in the human subject, and by Blondlot and others, in experiments upon the inferior animals; another is to make use of properly-prepared acidulated infusions of the mucous membrane of the stomach, which have been shown to have sensibly the same properties as the gastric juice, differing only in activity; and another is to examine from time to time the contents of the stomach after food has been taken. By all of these methods of study, it has been shown that the digestion of meat in the stomach is far from being complete. The parts of the muscular structure most easily attacked are the fibrous tissue which holds the muscular fibres together, with the sarcolemma, or sheath of the fibres themselves. If the gastric juice of the dog be placed in a vessel with finely-chopped lean meat and be kept in contact with it for a number of hours at from 80° to 100° Fahr., agitating the vessel occasionally so as to subject, as far as possible, every particle of the meat to its action, the filtered fluid will be found increased in density, its acidity diminished, and presenting all the evidences of having dissolved a considerable portion of the tissue. There always, however, will remain a certain portion which has not been dissolved. Its constitution is nevertheless materially changed; for it no longer possesses the ordinary character of muscular tissue, but easily breaks down between the fingers into a pultaceous mass. On subjecting this residue to microscopical examination, it is found not to contain any of the white inelastic fibres; and the fibres of muscular tissue, although presenting the well-marked and characteristic striæ, are broken into short pieces and possess very little tenacity. It is evidently only the muscular substance which remains; the connective tissue and the sarcolemma having been dissolved. These facts we have repeatedly noted, and, even on adding fresh juice to the undigested matter, we have been unable to dissolve it to any considerable extent, the residue not being sensibly diminished in quantity, and the muscular substance always presenting its characteristic striæ, on microscopical examination.

Although it is stated by many, in a general way, that the nitrogenized alimentary principles are digested by the gastric juice, a review of actual experiments will show that the digestion of meat in the stomach is substantially such as we have just indicated. Beaumont, in his experiments on artificial digestion, while he frequently states that the meat is completely digested, describes the mixture, after a digestion of eight or nine hours, as about the color of whey and depositing a fine sediment of a reddish color after standing for a few minutes. In no case does he distinctly state that meat is ever completely dissolved. Pappenheim examined animal matters, especially muscular tissue, in various stages of digestion by the gastric juice, and noted the disintegration of the tissue and division of the muscular fibres into fragments, but not the solution of the true muscular substance. Burdach describes the digestion of meat as consisting in the solution of its cellular tissue, which is dissolved, first separating the muscular fibres, and finally being converted into a pultaceous mass, more or less brown. The same facts, essentially, have been noted by Bernard in experiments with the gastric juice of different animals. This observer has found that the fluid from the stomach of the rabbit or the horse is much inferior, as regards the activity of its action upon meat, to the gastric juice of the dog. He compares the disintegrating process which takes place in the stomach to the action of boiling water in cooking.

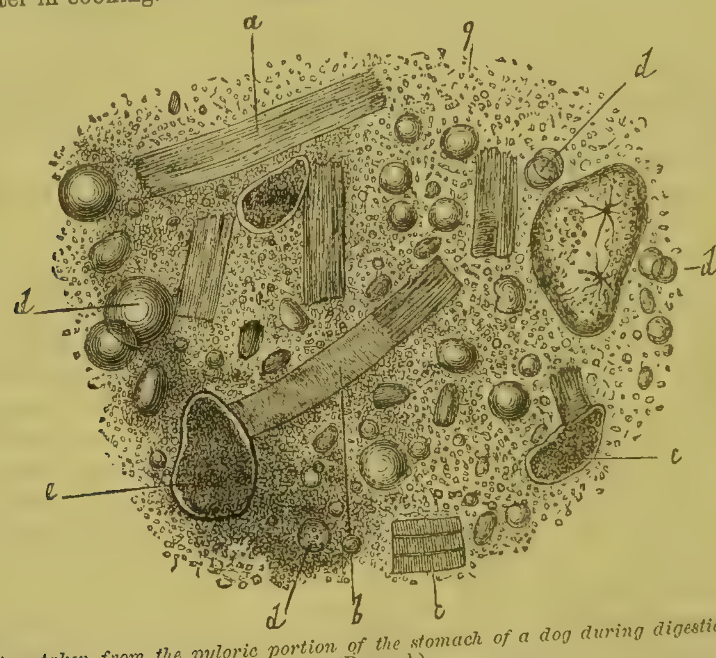


FIG. 62.—*Matters taken from the pyloric portion of the stomach of a dog during digestion of mixed food.* (Bernard.)

a, disintegrated muscular fibres, the striæ having disappeared; *b*, *c*, muscular fibres, in which the striæ have partly disappeared; *d*, *d*, *d*, globules of fat; *e*, *e*, *e*, starch; *g*, molecular granules.

Whether the gastric juice be entirely incapable of acting upon the muscular substance or not, the above-mentioned facts clearly show that muscular tissue is usually not completely digested in the stomach. The action in this organ is to dissolve out the intermuscular fibrous tissue and the sarcolemma, or sheath of the muscular fibres, setting the true muscular substance free and breaking it up into small particles. The mass of tissue is thus reduced to the condition of a thin, pultaceous fluid, which passes into the small intestine, where the process of digestion is completed. As far as a great part of the true muscular substance is concerned, the action in the stomach is preparatory and not final.

The constituents of the blood (albumen, corpuscles, etc.), which may be introduced in small quantity in connection with muscular tissue, are probably completely dissolved in the stomach.

Action upon Albumen, Fibrin, Caseine, and Gelatine.—Dr. Beaumont thought that raw albumen, or white of egg, became first coagulated in the stomach and was afterward dissolved; but this has been disproved by numerous other observers, who, however, have experimented chiefly on dogs. Reference to the experiments of Beaumont will show that the phenomena which he described as taking place in a mixture of equal parts of white of egg and gastric juice, kept at the temperature of the body for three hours, do not really indicate coagulation. He states that "in ten or fifteen minutes, small, white flocculi began to appear, floating about; and the mixture became of an opaque and whitish appearance. This continued slowly and uniformly to increase for three hours, at which time the fluid had become of a milky appearance; the small flocculi, or loose coagula, had mostly disappeared, and a light-colored sediment subsided to the bottom." If white of egg be mixed with equal parts of pure water and be gently stirred with a glass rod, the same small, white flocculi will make their appearance, and the mixture will become opaque and whitish. This is due to the disengagement of shreds of the membranes in which the clear albumen is contained; these being invisible in pure white of egg, from the fact that the two substances have the same refractive power. A very different appearance is presented when water containing even a small quantity of nitric acid is added to a liquid containing albumen. True coagulation then takes place, and the mixture becomes immediately filled with large, dense clots; or the mass may become nearly solidified, if the acid be added in sufficient quantity. Longet and Schiff injected a filtered watery mixture of albumen into the stomach of a dog through a fistulous opening and found that no coagulation took place.

The action of the gastric juice upon uncooked white of egg is to disintegrate its structure, separating and finally dissolving the membranous sacs in which the pure albumen is contained. It also acts upon the albumen itself, forming a new fluid substance, called albuminose, or albumen-peptone, which, unlike albumen, is not coagulated by heat or acids, but is precipitated by alcohol, tannin, and many of the metallic salts.

The digestion of raw or imperfectly-coagulated albumen takes place with considerable rapidity in the stomach. Beaumont gave St. Martin the white of two eggs when the stomach was empty and found that it had been completely disposed of in an hour and a half. The digestion of albumen in this form is more rapid than when it has been completely coagulated by heat.

Coagulated white of egg is almost if not entirely dissolved by the gastric juice. If a cube of albumen in this condition be subjected to the action of the gastric juice at the temperature of the body, taking care to agitate it occasionally, the edges and corners gradually become rounded, and nearly the whole mass finally breaks down and is dissolved, having previously become softened so that it may be easily crushed between the fingers. Usually, one or two points appear in the mass, which are acted upon with difficulty or may resist solution entirely. It is a matter of common as well as scientific observation, that eggs when hard-boiled are less easily digested than when they are soft-boiled or raw.

The products of the digestion of raw or of coagulated albumen (albumen-peptone) are essentially the same. It is probable that the entire process of digestion and absorption of albumen takes place in the stomach, and, if any pass out of the pylorus, the quantity is exceedingly small.

Fibrin, as distinguished from the so-called fibrin of the muscular tissue, or musculine, is not a very important article of diet. The action of the gastric juice upon it is more rapid and complete than upon albumen. The well-known action upon fibrin of water slightly acidulated with hydrochloric acid has led some physiologists to assume that the acid is the only constituent in the gastric juice necessary to the digestion of this principle;

but careful observations on the comparative action of acidulated water and of artificial or natural gastric juice show that the presence of the organic matter is necessary to the digestion of this as well as of other nitrogenized alimentary principles. The action of water containing a small proportion of acid is to render fibrin soft and transparent, frequently giving to the entire mass a jelly-like consistence. The result of the digestion of fibrin in the gastric juice, or in an acidulated fluid to which pepsin has been added, is its complete solution and transformation into a substance which is not affected by heat, acids, or by rennet.

The substance resulting from the action of gastric juice upon fibrin, called by Lehmann, fibrin-peptone, presents many points of similarity with the albumen-peptone, but nevertheless has certain distinctive characters. Lehmann, indeed, supposes that there are differences between the products of the digestion of all the various nitrogenized alimentary principles, sufficiently well marked to distinguish them from each other.

Liquid caseine is immediately coagulated by the gastric juice, by virtue both of the free acid and the organic matter. Once coagulated, caseine is acted upon in the same way as coagulated albumen. The caseine which is taken as an ingredient of cheese is digested in the same way. According to Lehmann, coagulated caseine requires a longer time for its solution in the stomach than most other nitrogenized substances; and it is stated by the same author, on the authority of Elsässer, that the caseine of human milk, which coagulates only into a sort of jelly, is more easily digested than caseine from cow's milk. The product of the digestion of caseine is a soluble substance, not coagulable by heat or the acids, called by Lehmann, caseine-peptone.

Gelatine is rapidly dissolved in the gastric juice, when it loses the characters by which it is ordinarily recognized, and no longer forms a jelly on cooling. This substance is much more rapidly disposed of than the tissues from which it is formed, and the products of its digestion in the gastric juice resemble the substances resulting from the digestion of the albuminoids generally.

Action on Vegetable Nitrogenized Principles.—These principles, of which gluten may be taken as the type, undoubtedly are chiefly, if not entirely digested in the stomach. Raw gluten is acted upon very much in the same way as fibrin, and cooked gluten behaves like coagulated albumen. Vegetable articles of food generally contain gluten in greater or less quantity, or principles resembling it, as well as various non-nitrogenized principles, and cellulose. The fact that these articles are not easily attacked in any portion of the alimentary canal, unless they have been well comminuted in the mouth, is shown by the passage of grains of corn, beans, etc., in the fæces. When properly prepared by mastication and insalivation, the action of the gastric juice is to disintegrate them, dissolving out the nitrogenized principles, freeing the starch and other matters so that they may be more easily acted upon in the intestines, and leaving the hard, indigestible matters, such as cellulose, to pass away in the fæces. The nitrogenized portions of bread are probably acted upon in the stomach in the same way and to the same extent as albumen, fibrin, and caseine.

Albuminose, or Peptones.

The product or the sum of the products of the digestion of nitrogenized alimentary principles in the stomach was first closely studied by Mialhe, who regarded the action of the gastric juice on all principles of this class as resulting in their transformation into a new substance which he called albuminose. Lehmann has since investigated the principles resulting from the action of the gastric juice on various nitrogenized matters and describes them under the name of peptones. It has been conclusively shown that stomach-digestion is not merely a solution of certain alimentary principles, but that these substances undergo very marked changes and lose the properties by which they are generally recognized. That the different principles resulting from this transformation resemble each other very closely is also undoubted; but there are differences in the chemical composition of the products of digestion of different principles, as well as differences, which have lately been noted, as regards their behavior with reagents.

Albuminose is a colorless liquid, with a feeble odor resembling that of meat. It is not coagulable by heat, acids, or by pepsin; a property which distinguishes it from almost all of the nitrogenized principles of food. It is coagulated, however, by many of the metallic salts, by chlorine, and by a solution of tannin, after it has been acidulated by nitric acid. On evaporating albuminose to dryness, the residue consists of a yellowish-white substance, resembling desiccated white of egg. This is soluble in water, when it regains its characteristic properties; but it is entirely insoluble in alcohol.

Lehmann found a great similarity between the substances resulting from the digestion of the various albuminoid bodies, and even those produced by the digestion of gluten, chondrine, and gelatinous tissues. He was unable to obtain the peptones free from mineral substances. In the condition of greatest purity in which they have been obtained, they have been found to be white, amorphous, odorless, with a mucous taste, very soluble in water, and insoluble in alcohol. Their watery solutions redden litmus. They combine readily with bases, forming neutral salts soluble in water. The differences between the various peptones are not as yet very well defined. Lehmann states that they always contain the same proportion of sulphur that existed in the albuminoid substances from which they are formed. According to this observer, the gastric juice transforms the various nitrogenized alimentary principles into these liquid substances, which are not easily coagulable and which present slight differences in chemical composition and general properties, varying with the principles from which they are formed. Those which have been most particularly described are fibrin-peptone, albumen-peptone, and caseine-peptone.

With even the imperfect knowledge which we have of the properties of albuminose, it is evident that stomach-digestion, aside from its function in preparing certain articles for the action of the intestinal fluids, does not simply liquefy certain of the alimentary principles, but changes them in such a way as to render them endosmotic and provides against the coagulation which is so readily induced in ordinary nitrogenized bodies. Albuminose passes through membranes with great facility, and, as we have seen, is not coagulable by heat or the acids.

Another, the most important and the essential change which is exerted by the gastric juice upon the albuminoids, is that by which they are rendered capable of assimilation by the system after their absorption. The important fact that pure albumen and gelatine, when injected into the blood, are not assimilable, but are rejected by the kidneys, was first demonstrated by Bernard and Barreswil. These observers found, also, that albumen and gelatine which had previously been digested in gastric juice were assimilated in the same way as though they had penetrated by the natural process of absorption from the alimentary canal. The same is true of caseine and fibrin. These facts, showing that something more is necessary in stomach-digestion than mere solution, point to pepsin as the important active principle in producing the peculiar modifications so necessary to proper assimilation of nitrogenized alimentary substances. The action which takes place is one of those ordinarily termed catalytic, in which the pepsin, acting as a ferment, induces certain peculiar changes. They are, however, an essential and the most important part of the action of the gastric juice, and the transformation into albuminose takes place in all nitrogenized principles which are liquefied in the stomach. As it is impossible for two catalytic processes to take place at the same time in any single organic substance, the more powerful always overcoming and taking the place of the weaker, it is evident that, when nitrogenized principles in process of decomposition are introduced into the stomach, the catalytic process of putrefaction must cease when the changes which occur in digestion become established. This explains the antiseptic properties of the gastric juice and the frequent innocuousness of animal substances in various stages of decomposition, when taken into the stomach.

Action of the Gastric Juice on Fats, Sugars, and Amylaceous Substances.—Beaumont does not say much with regard to the changes which fatty substances undergo in the stomach, except that they are "digested with great difficulty." All the recent observations on this subject show that these principles, when taken in the condition of oil, pass out at the pylorus unchanged. Most of the fatty constituents of the food are liquefied at the temperature of the body; and, when taken in the form of adipose tissue, the little vesicles in which the oleaginous matter is contained are dissolved, the fat is set free and melted, and floats in the form of great drops of oil on the alimentary mass. The action of the stomach, then, seems to be to prepare the fats for digestion, chiefly by dissolving the adipose vesicles, for the complete digestion which takes place in the small intestine.

The varieties of sugar of which glucose is the type undergo little if any change in digestion and are probably for the most part directly absorbed by the mucous membrane of the stomach. This is not the case, however, with the varieties of sugar classed with cane-sugar. It has been shown that cane-sugar injected into the veins of a living animal is not assimilated by the system but is immediately rejected by the kidneys. When, however, it has been changed into glucose by the action of a dilute acid or by digestion in the gastric juice, it no longer behaves as a foreign substance and does not appear in the urine. This leads to a consideration of the changes which cane-sugar undergoes in the stomach. Experiments have shown that this variety of sugar, after being digested for several hours in the gastric juice, is slowly converted into glucose. This action does not depend upon any constituent of the gastric juice except the free acid; and an exceedingly dilute mixture of hydrochloric acid had an equally marked effect. Experiments in artificial digestion have shown that cane-sugar is transformed into glucose by the gastric juice very slowly, the action of this fluid in no way differing from that of very dilute acids. In the natural process of digestion, this action may take place to a certain extent; but it is not shown to be constant or important, and we must look to intestinal digestion for the rapid and efficient transformation of cane-sugar.

The action of gastric juice, unmixed with saliva, upon starch is entirely negative, as far as any transformation into sugar is concerned. When the starch is enclosed in vegetable cells, it is set free by the action of the gastric juice upon the nitrogenized parts. Raw starch, in the form of granules, becomes hydrated in the stomach, on account of the elevated temperature and the acidity of the contents of the organ. This is not the form, however, in which starch is generally taken by the human subject; but when it is so taken, the stomach evidently assists in preparing it for the more complete processes of digestion which are to take place in the small intestine.

Cooked or hydrated starch, the form in which it exists in bread, farinaceous preparations generally, and ordinary vegetables, is not affected by the pure gastric juice and passes out at the pylorus unchanged. It must be remembered, however, that the gastric juice does not prevent a continuance of the action induced by the saliva; and experiments have shown that gastric juice taken from the stomach, when it contains a notable quantity of saliva, has, to a certain extent, the power of transforming starch into sugar. It has already been remarked that, with regard to this question, experiments on dogs, as these animals do not naturally take starch as food, do not correspond with observations on the human subject.

The changes which vegetable acids and salts, the various inorganic constituents of food, and the liquids which come under the head of drinks undergo in the stomach are very slight. Most of these principles can hardly be said to be digested; for they are either liquid or in solution in water and are capable of direct absorption and assimilation. With regard to most of the inorganic salts, they either exist in small quantity in the ordinary water taken as drink or are united with organic nitrogenized principles. In the latter case, they become intimately combined with the organic principles resulting from stomach-digestion. We have already seen that the various peptones have been found to contain the same inorganic constituents which existed in the nitrogenized principles from which they are formed.

Some discussion has arisen with regard to the action of the fluids of the stomach upon the phosphate and the carbonate of lime, salts which are considered nearly if not entirely insoluble. The action upon these principles is interesting, as they are essential constituents of the osseous tissues. Observations in both natural and artificial digestion have shown that the calcareous constituents of bone are, to a certain extent, dissolved in the gastric juice. Bones are digested to a considerable extent in the stomach, although the greater part passes through the alimentary canal and is discharged unchanged in the fæces. Beaumont has shown this to be true in the human subject by experiments which he performed, out of the body, with gastric juice taken from St. Martin. In these observations, after a certain portion of the bone had been dissolved, the action was increased by the addition of fresh gastric juice. In the natural process of digestion, the solution of the calcareous elements of bone is more rapid than in artificial digestion, from the fact that the juice is being continually absorbed and secreted anew by the mucous membrane of the stomach.

Duration of Stomach-Digestion.

Now that the relative importance of the stomach and the small intestines in digestion is more fully understood, less interest is attached to the length of time required for the action of the gastric juice upon different articles of food than formerly, when the stomach was regarded as the principal, if not the sole digestive organ. It was thought at one time that the food was converted in the stomach into a pultaceous mass called chyme, which passed into the intestine, where the assimilable portion, the chyle, was separated and absorbed by the lacteals. Beaumont, in preparing the elaborate table which has been so much quoted, conceived that the simple action of the gastric juice represented the chief part of the digestive process; and that it was possible, from experiments with this fluid, to ascertain the digestibility of different articles. From this point of view, he regarded fatty substances, which are now known to be digested exclusively in the small intestines, as requiring a very long time for their digestion.

Understanding, as we do, that comparatively few articles, and these belonging exclusively to the class of organic nitrogenized principles, are completely dissolved in the stomach, it is evident that the length of time during which food remains in this organ, or the time occupied in the solution of food by gastric juice, out of the body, does not represent the absolute digestibility of different articles. It is, nevertheless, an interesting and an important question to ascertain, as nearly as possible, the duration of stomach-digestion.

There has certainly never been presented so favorable an opportunity for determining the duration of stomach-digestion as in the case of St. Martin. From a great number of observations made on digestion in the stomach itself, Beaumont came to the conclusion that "the time ordinarily required for the disposal of a moderate meal of the fibrous parts of meat, with bread, etc., is three to three and a half hours." The observations of Prof. F. G. Smith, made upon St. Martin many years later, give two hours as the longest time that aliments remained in the stomach. In a remarkable case of intestinal fistula, reported by Prof. Busch, of Bonn, it was noted that food began to pass out of the stomach into the intestines fifteen minutes after its ingestion and continued to pass for three or four hours, until the stomach was emptied.

Undoubtedly, the duration of stomach-digestion varies in different individuals and is greatly dependent upon the kind and quantity of food taken, conditions of the nervous system, exercise, etc. As a mere approximation, the average time that food remains in the stomach after an ordinary meal may be stated to be from two to four hours.

Digestibility of Different Aliments in the Stomach.—We are indebted to Beaumont for nearly all that is positively known regarding the facility with which different articles are disposed of in the stomach. While it is fully understood that most of the substances experimented upon by him are not completely digested by the gastric juice, and although he was often wrong in assuming that articles of food were digested when they had not become completely liquefied and consequently endosmotic, the table which he prepared with so much care was the result of such conscientious and extended research, that it must always be recognized as of great value. Nearly all of the results given in the table are derived from experiments frequently repeated and "performed under the naturally healthy condition of the stomach and ordinary exercise." They show the mean time employed in the digestion, in the stomach, of most of the ordinary articles of food, in the person of a healthy young man of good digestive powers. Of course it must be understood that there are important peculiarities in different individuals, which could not be considered. As many of the alimentary substances experimented upon are but slightly acted on by the gastric juice, it has been thought proper, in making the selections from the table, to discard all articles which are mainly digested in the small intestine. With these modifications, therefore, the following table may be taken as representing the comparative rapidity with which most of the ordinary nitrogenized articles are acted upon in the stomach; they being either completely dissolved, and probably directly absorbed by its mucous membrane, or prepared for the action of the intestinal fluids, passing gradually out at the pylorus. It must be remembered, however, that slow digestion does not always indicate that the process is difficult, and the action of the gastric fluids upon many articles which apparently give no trouble in digestion is by no means rapid.

Table showing the Digestibility of various Alimentary Substances in the Stomach. (Beaumont.)

Articles of Diet.	Mode of Preparation.	Hours. Min.	Articles of Diet.	Mode of Preparation.	Hours. Min.
Milk	Boiled	2·00	Chicken, full grown	Fricasseed	2·45
do.	Raw	2·15	Fowls, domestic	Boiled	4·00
Eggs, fresh	do.	2·00	do. do.	Roasted	4·00
do. do.	Whipped	1·30	Ducks, domesticated	do.	4·00
do. do.	Roasted	2·15	do. wild	do.	4·30
do. do.	Soft-boiled	3·00	Soup, barley	Boiled	1·30
do. do.	Hard-boiled	3·30	do. bean	do.	3·00
do. do.	Fried	3·30	do. chicken	do.	3·00
Custard	Baked	2·45	do. mutton	do.	3·30
Codfish, cured dry	Boiled	2·00	do. oyster	do.	3·30
Trout, salmon, fresh	do.	1·30	do. beef, vegetables, and bread	do.	4·00
do. do. do.	Fried	1·30	do. marrow-bones	do.	4·15
Bass, striped, do.	Broiled	3·00	Pigs' feet, soused	do.	1·00
Flounder, do.	Fried	3·30	Tripe, do.	do.	1·00
Catfish, do.	do.	3·30	Brains, animal	do.	1·45
Salmon, salted	Boiled	4·00	Spinal marrow, animal	do.	2·40
Oysters, fresh	Raw	2·55	Liver, beeves', fresh	Broiled	2·00
do. do.	Roasted	3·15	Aponeurosis	Boiled	3·00
do. do.	Stewed	3·30	Heart, animal	Fried	4·00
Venison steak	Broiled	1·35	Cartilage	Boiled	4·15
Pig, sucking	Roasted	2·30	Tendon	do.	5·30
Lamb, fresh	Broiled	2·30	Hash, meat and vegetables	Warmed	2·30
Beef, fresh, lean, rare	Roasted	3·00	Sausage, fresh	Broiled	3·20
Beef-steak	Broiled	3·00	Gelatine	Boiled	2·30
Beef, fresh, lean, dry	Roasted	3·30	Cheese, old, strong	Raw	3·30
do. with mustard, etc.	Boiled	3·10	Green corn and beans	Boiled	3·45
do. with salt only	do.	3·36	Beans, pod	do.	2·30
do.	Fried	4·00	Parsnips	do.	2·30
Mutton, fresh	Broiled	3·00	Potatoes, Irish	Roasted	2·30
do. do.	Boiled	3·00	do. do.	Baked	2·30
do. do.	Roasted	3·15	do. do.	Boiled	3·30
Veal, fresh	Broiled	4·00	Cabbage, head	Raw	2·30
do. do.	Fried	4·30	do. do. with vinegar	do.	2·00
Pork, steak	Broiled	3·15	do. do.	Boiled	4·30
do. fat and lean	Roasted	5·15	Carrot, orange	do.	3·13
do. recently salted	Raw	3·00	Turnips, flat	do.	3·30
do. do.	Stewed	3·00	Beets	do.	3·45
do. do.	Broiled	3·15	Bread, corn	Baked	3·15
do. do.	Fried	4·15	do. wheat, fresh	do.	3·30
do. do.	Boiled	4·30	Apples, sweet, mellow	Raw	1·30
Turkey, wild	Roasted	2·18	do. sour, do.	do.	2·00
do. domesticated	Boiled	2·25	do. do. hard	do.	2·50
do. do.	Roasted	2·30			
Goose, wild	do.	2 30			

Most of the facts recorded in the above table are in accordance with the popular ideas regarding the digestibility of various articles, based upon general experience. With these as a guide, the following may be taken as a summary of what is known regarding the facility with which different articles are disposed of in the stomach:

Milk is one of the articles digested in the stomach with greatest ease. Its highly-nutritive properties and the variety of principles which it contains render it extremely valuable as an article of diet, particularly when the digestive powers are impaired and when it is important to supply the system with considerable nutriment. Eggs are likewise highly nutritious and are easily digested. Raw and soft-boiled eggs are more easily digested than hard-boiled. Whipped eggs are apparently disposed of with great facility. As a rule, the flesh of fish is more easily digested than that of the warm-blooded animals. Oysters, especially when raw, are quite easy of digestion. The flesh of mammals seems to be more easily digested than the flesh of birds. Of the different kinds of meat, venison, lamb, beef, and mutton are easily digested, while veal and fat roast-pork are digested with difficulty. Soups are generally very easily digested. The animal substances which were found to be digested most rapidly, however, were tripe, pigs' feet, and brains. Vegetable articles are represented in the table as being digested in about the same time as ordinary animal food; but a great part of the digestion of these substances takes place in the small intestine. Bread is digested in about the time required for the digestion of the ordinary meats.

Circumstances which influence Stomach-Digestion.

The various conditions which influence stomach-digestion, except those which relate exclusively to the character or the quantity of food, operate mainly by influencing the quantity and quality of the gastric juice. It is seldom, if ever, that temperature has any influence; for the temperature of the stomach in health does not present variations sufficient to have any marked effect upon digestion. Experiments in artificial digestion have shown that alimentary substances are most vigorously acted upon when maintained in contact with gastric juice at or near 100° Fahr.

As a rule, gentle exercise, conjoined with repose or agreeable and tranquil occupation of the mind, is more favorable to digestion than absolute rest. Violent exercise or severe mental or physical exertion is always undesirable immediately after the ingestion of a large quantity of food, and, as a matter of common experience, has been found to retard digestion. Sleep, if light and taken in the sitting posture, seems almost necessary to easy digestion in many persons; but it should be continued for only a few minutes. A prolonged and deep sleep immediately after a full meal is almost always injurious, and extraordinary heaviness at that time is generally an indication that too much food has been taken.

The effects of sudden and considerable loss of blood upon stomach-digestion are very marked. After a full meal, the whole alimentary tract is deeply congested, and this condition is undoubtedly necessary to the secretion, in proper quantity, of the various digestive fluids. When the entire quantity of blood in the economy is greatly diminished from any cause, there is a difficulty in supplying the amount of gastric juice necessary for a very full meal, and disorders of digestion are apt to occur, especially if a large quantity of food have been taken. This is also true in inanition, when the quantity of blood is greatly diminished. In this condition, although the system constantly craves nourishment and the appetite is frequently enormous, food should be taken in small quantities at a time.

As a rule, children and young persons digest food which is adapted to them more easily and in larger relative quantity than those in adult life or in old age; but, ordinarily, in old age, the digestive processes are carried on with more vigor and regularity than the other vegetative functions, such as general assimilation, circulation, or respiration.

Influence of the Nervous System on the Stomach.—It is well known that mental emotions frequently have a marked influence on digestion, and this, of course, can take place only through the nervous system. Of the two nerves which are distributed to the stomach, the pneumogastric has been the more carefully studied, experiments upon the sympathetic being difficult and unsatisfactory. Although the complete history of the influence of the pneumogastric nerves upon digestion belongs to the section on the nervous system, it will be interesting in this connection to consider briefly some of the facts which have been ascertained with regard to the influence which these nerves exert upon the stomach.

After section of the pneumogastric nerves in the neck, acts of deglutition are apparently performed, but the food usually collects in and distends the paralyzed œsophagus and does not pass to the stomach. It is not surprising, therefore, that the first experiments upon the influence of the pneumogastrics on digestion should have been contradictory, some contending that section of the nerves arrested stomach-digestion, while others maintained that the nerves had little or no influence upon the stomach. It is evident that, without an appreciation of the effects of section of the pneumogastrics upon deglutition, observations on the influence of their section upon stomach-digestion would be of little value.

The experiments of Longet seem to show that, while section of the pneumogastrics in the neck undoubtedly diminishes the secretion of gastric juice, the production of this fluid is not entirely arrested. He states that in dogs, one or two days after section of the nerves, he found the lacteals filled with chyle after milk had been passed into the stomach; but it is now well known that chyle is in great part, if not entirely formed in the intestinal canal, without the intervention of the stomach. Another experiment, however, is more interesting. After section of the pneumogastrics, having exposed the mucous membrane of the stomach, he found that an acid fluid appeared in parts which were subjected to mechanical or galvanic irritation. The general results of his experiments on this subject were that, after the division of both pneumogastric nerves, small quantities of food could be digested in the stomach, but that a considerable mass was only chymified on the surface, the centre not undergoing any alteration. This he attributes, not so much to arrest of secretion of the gastric juice, as to paralysis of the movements of the stomach, which, when the mass of food is considerable, are necessary in order to expose all parts to the action of the gastric juice.

The experiments of Bernard on this subject are very clear and satisfactory. When the mucous membrane of the stomach was turgid with blood, the animal (a dog) being in full digestion and provided with a large gastric fistula so that the changes which might take place in the stomach could be readily observed, the pneumogastrics were divided in the neck. At once the mucous membrane became pale and flaccid, and the secretion of gastric juice was arrested. When the animal died after section of the pneumogastrics during digestion, it was remarked that the absorption of chyle seemed to have been arrested, the lacteals being found to contain coagulated chyle even as far as the villi of the intestines. According to these experiments, the action of gastric juice which might exist in the stomach at the time of section of the pneumogastrics would continue, but no new fluid is secreted; and, if the fluid thus remaining in the stomach be neutralized, digestion is immediately arrested. In one experiment in which the pneumogastrics had been divided, having previously emptied the stomach, Bernard introduced meat finely divided. The next day, the meat had a distinctly-ammoniacal odor and an alkaline reaction, the result of spontaneous decomposition. These experiments show only an immediate arrest of the secretion of the gastric juice. In certain exceptional instances, in which animals survive the section of both nerves for a number of days or sometimes even recover, it has been noted that, after a few days, an acid secretion again takes place in the stomach.

Although much confusion exists in the earlier observations on the effects of section of the pneumogastrics upon the stomach, the conclusions to be drawn from recent experiments are tolerably definite.

There can be no doubt that division of both these nerves produces immediate and grave disorder in the process of stomach-digestion, amounting, it is more than probable, to complete arrest of the secretion of the gastric juice. Its secretion may be induced again by local stimulation, but the quantity is always greatly diminished. Under these circumstances, it is possible that very small quantities of food may be digested in the stomach a day or two after the operation; and, if the animal survive for a considerable time, the secretion may be to a certain extent reëstablished. Serious trouble in stomach-digestion is produced by the paralysis of the muscular coats of the stomach consequent upon section of both pneumogastrics.

Movements of the Stomach.—As the articles of food are passed into the stomach by the acts of deglutition, the organ gradually changes its form, size, and position. When the stomach is empty, the opposite surfaces of its lining membrane are in contact in many parts and are thrown into numerous longitudinal folds. As the organ is distended, these folds are effaced, the stomach itself becoming more rounded; and, as the two ends with the lesser curvature are comparatively immovable, the whole organ undergoes a movement of rotation, by which the anterior face becomes superior and is applied to the diaphragm. At this time the great pouch has nearly filled the left hypochondriac region, the greater curvature looks anteriorly, and comes in contact with the abdominal walls. Aside from these changes, which are merely due to the distention, the stomach undergoes important movements, which continue until its contents have been dissolved and absorbed or have passed out at the pylorus. But while these movements are taking place, the two orifices are guarded, so that the food shall remain for the proper time exposed to the action of the gastric juice. We have already noted the rhythmical contractions of the lower extremity of the œsophagus, by which regurgitation of food is prevented; and the circular fibres, which form a thick ring at the pylorus, are constantly contracted, so that, at least during the first periods of digestion, only liquids and that portion of food which has been reduced to a pultaceous consistence can pass into the small intestine. It is well known that this resistance at the pylorus does not endure indefinitely, for indigestible articles of considerable size, such as stones, have been passed by the anus after having been introduced into the stomach; but observation has shown that masses of digestible matter are passed by the movements of the stomach to the pylorus, over and over again, and that they do not find their way into the intestine until they have become softened and broken down.

The contractions of the walls of the stomach are of the kind characteristic of the non-striated muscular fibres. If the finger be introduced into the stomach of a living animal during digestion, it is gently but rather firmly grasped by a contraction, which is slow and gradual, enduring for a few seconds, and as slowly and gradually relaxing and extending to another part. The movements during digestion undoubtedly present certain differences in different animals; but there can be no doubt that the phenomenon is universal. In dogs, when the abdomen is opened soon after the ingestion of food, the stomach appears pretty firmly contracted on its contents. In a case reported by Todd and Bowman, in the human subject, in which the stomach was very much hypertrophied and the walls of the abdomen were very thin, the vermicular movements could be distinctly seen. These movements were active, resembling the peristaltic movements of the intestines, for which, indeed, they were mistaken, as the nature of the case was not recognized during life. No argument, therefore, seems necessary to show that, during digestion, the stomach is the seat of tolerably active movements.

A peculiarity in the movements of the stomach, which has been repeatedly observed in the lower animals, particularly dogs and cats, and in certain cases has been confirmed in the human subject, is that, at about the junction of the cardiac two-thirds with the pyloric third, there is frequently a transverse band of fibres so firmly contracted as to divide the cavity into two almost distinct compartments. It has also been noted that the contractions in the cardiac division are much less vigorous than near the pylorus; the stomach seeming simply to adapt itself to the food by a gentle pressure as it remains in the great pouch, while, in the pyloric portion, divided off as it is by the hour-glass contraction above-mentioned, the movements are more frequent, vigorous, and expulsive. We must again refer, however, to the observations of Beaumont for the only accurate description of the movements of the stomach, as they take place during digestion in the human subject.

The experiments of Beaumont were generally made with the subject lying on the right side, and the movements of the stomach were observed by following with the eye a particular morsel of food as it passed along, or by introducing the bulb of a thermometer into the organ and allowing it to move with the alimentary mass. It was invariably found that the movements of the thermometer-bulb were the same as those observed by identifying and following a particular portion of food. As the alimentary bolus enters by the cardiac opening, it turns to the left, descends into the greater pouch, and follows the greater curvature to the pyloric end. It then returns to the cardiac orifice by the lesser curvature and takes again the same course as before. While these revolutions, so to speak, of the alimentary mass are going on, the food is turned over and over, so that it becomes intimately mixed with the digestive fluids and subjected to a certain amount of trituration. This action is undoubtedly of great importance, as fresh portions of food are thereby successively exposed to the action of the gastric juice, and the boluses, with their particles agglutinated to a certain extent in the mouth, are disintegrated and penetrated with the gastric fluid in every part.

A marked difference was observed between the movements in the cardiac and in the pyloric portion. When the thermometer-bulb arrived at the contracted septum, which was three or four inches from the pyloric end, it was at first stopped by the forcible contraction; but, in a short time, there was a gentle relaxation which allowed it to pass, when it was drawn quite forcibly for three or four inches toward the pyloric opening. When in this portion of the stomach, the bulb was firmly grasped and made to undergo a spiral motion; and, if drawn forcibly out, it gave to the fingers the sensation of being held by a strong suction force. As soon as relaxation occurs, the bulb is passed back to the seat of stricture, and, when pulled through this, it moves freely in the great cavity. Each one of these revolutions was found to occupy from one to three minutes. They were slower at first than after digestion had been somewhat advanced.

The mechanism of the movements of the stomach is easily appreciated when we consider the number and varied direction of the fibres which form the muscular coat of the stomach, and the fact that the stomach, when distended, is more or less displaced with every movement of the diaphragm. It is easy to understand, also, how, in the pyloric portion, where the muscular fibres are thickest and the cavity is elongated and comparatively small, the movements should be more vigorous and expulsive than in the rest of the organ. We have already alluded to the fact that the movements of the stomach are animated by the pneumogastric nerves and become arrested when both these nerves are divided.

As the result chiefly of the observations of Beaumont, the following may be taken as a summary of the physiological movements of the stomach in digestion:

The stomach normally undergoes no movements until food is passed into its cavity. When food is received, at the same time that the mucous membrane becomes congested and the secretion of gastric juice commences, contractions of the muscular coat begin, which are slow and irregular during the commencement of stomach-digestion, but become more vigorous and regular as the process advances. After digestion has become fully established, the stomach is generally divided, by the firm and almost constant contraction of a transverse band of fibres, into a cardiac and a pyloric portion; the former occupying about two-thirds, and the latter, one-third of the length of the organ. The contractions of the cardiac division of the stomach are uniform and rather gentle; while, in the pyloric division, they are intermittent and more expulsive. The effect of the contractions of the stomach upon the food contained in its cavity is to subject it to a tolerably uniform pressure, with a certain amount of trituration and agitation, in the cardiac portion, the general tendency of the movement being toward the pylorus along the greater curvature, and back from the pylorus toward the great pouch along the lesser curvature. At the constricted part, which separates the cardiac from the pyloric portion, there is an obstruction to the passage of the food until it has been sufficiently acted upon by the secretions in the cardiac division to have become reduced to a pultaceous consistence. The alimentary mass then passes into the pyloric division, and, by a more powerful contraction than occurs in other parts of the stomach, it is passed into the small intestine. This completes the distinction between the two portions of the stomach, the cardiac division only, as we have already seen, possessing a mucous membrane capable of secreting the true solvent gastric juice.

The revolutions of the alimentary mass, thus accomplished, take place slowly, by gentle and persistent contractions of the muscular coat; the food occupying from one to three minutes in its passage entirely around the stomach. Every time that a revolution is accomplished, the contents of the stomach are somewhat diminished in quantity; probably, in a slight degree, from absorption of digested mater by the stomach itself, but chiefly by the gradual passage of the softened and disintegrated mass into the small intestine. This process continues until the stomach is emptied, occupying a period of from two to four hours; after which, the movements of the stomach cease until food is again introduced.

Regurgitation of Food, and Eructation.

Regurgitation of part of the contents of the stomach, in the human subject, although of frequent occurrence, particularly in early life, is not strictly a physiological act; and this is always due either to overloading of the stomach or to some pathological condition. But in some of the inferior animals this is habitual; a certain class, called ruminants, regularly passing the food, after the first deglutition, in small quantities from the paunch into the mouth, where it undergoes a second mastication and is only then permitted to pass to the secreting stomach and the rest of the alimentary canal. Animals of this class, examples of which are the ox, sheep, goat, camel, and the deer tribe, are invariably herbivorous and take into the stomach a large bulk of matter from which is elaborated a comparatively small quantity of nutriment. During the period when they are nourished by milk, rumination does not take place.

Considerable interest is attached to the function of rumination in the inferior animals, in connection with human physiology, from the fact that an analogous process has sometimes been observed in the human subject; though this is rare and is generally connected with a pathological condition. Such cases have been often quoted, and, in the earlier works on physiology, were frequently exaggerated; but, a few instances, well authenticated, are on record in which rumination had become habitual. A very remarkable case of this kind is reported by Home. The subject was an idiot-boy, aged nineteen years, who had an appetite so ravenous that it became necessary to restrict the quantity of food. At dinner he ordinarily ate about a pound and a half of meat and vegetables, swallowing the whole in two minutes. He began to chew the cud at the end of a quarter of an hour. The muscles of the throat could be seen to contract when the bolus was passed back to the mouth. He chewed the food by two or three movements of the jaws and then swallowed it again. This was repeated at intervals for half an hour, during which time he was always more quiet than usual. The intellect was so feeble that it was impossible to ascertain whether the rumination were voluntary or involuntary. One of the cases of rumination most frequently referred to is that of M. Cambay, who studied the phenomena in his own person and made it the subject of an inaugural thesis; and another is the case of the brother of M. P. Bérard. In these instances, as far as could be ascertained from the sensations during the act, the regurgitation of food was effected by persistent contractions of the muscular walls of the stomach, assisted by a slight and almost involuntary contraction of the abdominal muscles and diaphragm. It is stated by Cambay that, in his case, the taste of the articles of food was not modified, "but that it is with something of a sense of pleasure that the ruminator thus causes to return to the mouth the aliments that he has taken into the stomach, which makes them undergo a new trituration."

Rumination in the human subject is not a physiological act. It is evident that the substances returned to the mouth are not usually impregnated with the gastric juice, for they have not the disagreeable acid taste of ordinary vomited matters. The acts are generally preceded by a sense of fulness in the stomach, and their mechanism is probably nearly the same as that of the regurgitation of small quantities of milk from the distended stomachs of young children, which is so common. In the person of Cambay, the first act was said to be voluntary, but succeeding ones were not under the control of the will. Undoubtedly, the faculty of regurgitating the food may be improved by practice, and we have known of an instance in which it was apparently cultivated as an accomplishment.

The mechanism of regurgitation of portions of the contents of the stomach, aside from instances simulating rumination, has been so often alluded to that it demands in this connection but a passing mention. In some persons, this act may be accomplished by a voluntary muscular effort, especially when the stomach is overloaded. It occasionally happens, when the stomach is somewhat distended, that a small portion of its contents suddenly finds its way to the mouth without even the consciousness of the individual. The muscular contraction which produces this slight regurgitation is so insignificant that there must necessarily have been some relaxation at the cardiac opening of the stomach, which under ordinary conditions is, as we know, firmly closed. The act is then produced, in part by a slight contraction of the abdominal muscles and diaphragm, and in part by contractions of the stomach itself and anti-peristaltic movements of the œsophagus. It has nothing of the violent, expulsive character of true vomiting, which is produced by the spasmodic and involuntary contraction of the abdominal muscles and diaphragm, the stomach being passive.

The discharge of gases from the œsophagus by the mouth, accompanied with a peculiar and characteristic sound, is very common. This is usually accomplished without any marked contraction of the muscles concerned in vomiting and evidently requires very little force. Usually, the cardia is so effectually closed as to prevent the passage even of gases; and, in eructation, there must be a temporary relaxation of this opening. When thus relaxed, the act is accomplished chiefly by contractions of the stomach and œsophagus. It is generally accompanied or preceded by sensible convulsive movements of the œsophagus, involving, possibly, contractions of its longitudinal fibres, which would favor relaxation of the cardiac opening. Although it is usually involuntary, this act is sometimes under the control of the will. When it occurs, while it is difficult or impossible to prevent the discharge of the gas, the accompanying sound may be readily suppressed. Eructation is frequently a matter of habit, which in many persons becomes so developed by practice that the act may be performed voluntarily at any time.

CHAPTER IX.

INTESTINAL DIGESTION.—DEFÆCATION.

Physiological anatomy of the small intestine—Glands of Brunner—Intestinal tubules, or follicles of Lieberkühn—Solitary glands, or follicles, and the patches of Peyer—Intestinal juice—General properties of the intestinal juice—Action of the intestinal juice in digestion—Pancreatic juice—Action of the pancreatic juice in digestion—Destruction of the pancreas—Cases of fatty diarrhœa—Action of the pancreatic juice upon starchy, saccharine, and nitrogenized principles—Action of the bile in digestion—Biliary fistula—General constitution of the bile—Variations in the flow of bile—Movements of the small intestine—Peristaltic and antiperistaltic movements—Function of the gases in the small intestine—Influence of the nervous system upon the peristaltic movements—Physiological anatomy of the large intestine—Digestion in the large intestine—Contents of the large intestine—Composition of the fæces—Excretine and excretoleic acid—Stercorine—Movements of the large intestine—Defæcation—Gases found in the alimentary canal.

Physiological Anatomy of the Small Intestine.

The small intestine, so called on account of its small size as compared with the rest of the intestinal tract, is the long, cylindrical tube which occupies the greatest part of the abdominal cavity. This must now be regarded as the most important division of the digestive system; and its physiological anatomy, together with that of the great glands which discharge their secretions into its cavity, is indispensable as an introduction to the study of intestinal digestion. As it is in the small intestine that the final elaboration of most of the alimentary principles takes place, and here, also, that these principles are taken into the circulating fluid, we shall find, in our study of its anatomy, certain parts which are concerned in digestion, and others which, as far as we know, are connected only with the function of absorption. It will be most convenient, however, to consider, in this connection, all the structures found in the small intestine which possess physiological interest.

The small intestine, extending from the pyloric extremity of the stomach to the ileocæcal valve, is held to the spinal column by a double fold of serous membrane, called the mesentery. As the peritoneum which lines the cavity of the abdomen passes from either side to the spinal column it comes together in a double fold just in front of the great vessels along the spine, and, passing forward, splits again into two layers, which become continuous with each other and enclose the intestine, forming its external coat. The width of the mesentery is usually from three to four inches; but, at the commencement and the termination of the small intestine, it suddenly becomes shorter, binding the duodenum and that portion of the intestine which opens into the caput coli closely to the subjacent parts. The mesentery thus keeps the intestine in place but allows of a certain amount of motion, so that the tube may become convoluted, accommodating itself to the size and form of the abdominal cavity. The form of these convolutions is irregular and is continually changing.

The length of the small intestine, *in situ*, is probably from fifteen to eighteen feet (Sappey); but the canal is very distensible, and its dimensions are subject to constant variations. When separated from the mesentery and measured without stretching, its length has been found to be, on an average, about twenty feet. Its diameter is about one and a quarter inch.

The small intestine has been divided into three portions, which present anatomical and physiological peculiarities, more or less marked. These are the duodenum, the jejunum, and the ileum.

The duodenum has received its name from the fact that it is about the length of the breadth of twelve fingers, or from eight to ten inches. This portion of the intestine is considerably wider than the constricted, pyloric end of the stomach, with which it is continuous, and is also much wider than its continuation, the jejunum. It presents a curve, which is ordinarily described by anatomists as consisting of three portions. The first, called the hepatic or ascending portion, is about two inches in length. This is much less firmly fixed by its peritoneal attachment than the other portions and is nearly covered by the serous membrane. Its direction is outward, backward, and slightly upward. Turning downward, and a little inward, it merges into the second, called the descending

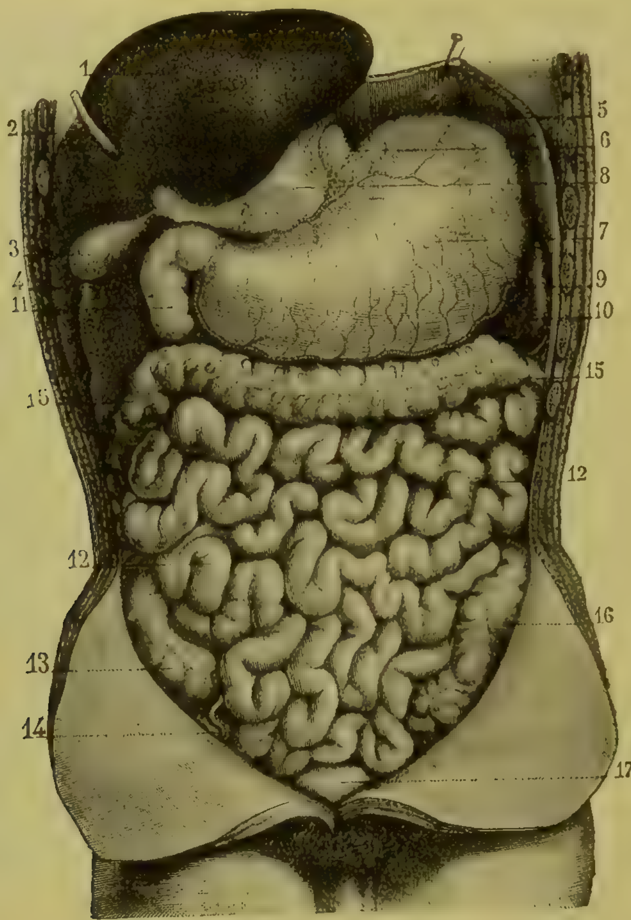


FIG. 63.—*Stomach, liver, small intestine, etc.* (Sappey.)
1, *inferior surface of the liver*; 2, *round ligament of the liver*; 3, *gall-bladder*; 4, *superior surface of the right lobe of the liver*; 5, diaphragm; 6, lower portion of the œsophagus; 7, *stomach*; 8, *gastro-hepatic omentum*; 9, spleen; 10, *gastro-splenic omentum*; 11, *duodenum*; 12, 12, *small intestine*; 13, *cæcum*; 14, *appendix vermiformis*; 15, 15, *transverse colon*; 16, *sigmoid flexure of the colon*; 17, urinary bladder.

or vertical portion, the length of which is about three inches. This is covered with peritoneum only on its anterior surface and is somewhat more firmly attached than the ascending portion. The intestine then makes a second bend, and the third or the transverse portion is horizontal in its course, passing across the spine to the left hypochondrium. This portion is about five inches in length. It is narrower than the others, is but partially covered by peritoneum, and is more firmly bound down than any other part of the small intestine.

The coats of the duodenum, like those of the other divisions of the intestinal tube, are three in number. Commencing externally, we have the serous, or peritoneal coat, which has already been described. The middle, or muscular coat is composed of the involuntary, or unstriped muscular fibres, such as exist in the stomach, arranged in two layers. The external, longitudinal layer is not very thick, and the direction of its fibres can be made out easily only at the outer portions of the tube opposite the attachment of the mesentery. Near the mesenteric border, the fibres are very faint. This is true throughout the whole of the small intestine; although the fibres are most numerous in the duodenum. The internal, circular, or transverse layer of fibres is considerably thicker than the longitudinal layer. These fibres encircle the tube, running, for the most part, at right angles to the external layer, but some of them having rather an oblique direction. The circular layer is thickest in the duodenum, diminishing gradually in thickness to the middle of the jejunum, but after that maintaining a nearly uniform thickness throughout the canal to the ileo-cæcal valve.

The jejunum, the second division of the small intestine, is continuous with the duodenum. It presents no well-marked line of separation from the third division, but is generally considered to include the upper two-fifths of the small intestine, the lower three-fifths being called the ileum. It has received the name jejunum from the fact that it is almost always found empty after death. This portion of the intestine presents no important peculiarities as regards its peritoneal and muscular coat.

The ileum is somewhat narrower and thinner than the jejunum, otherwise possessing no marked peculiarities except in the structure of its mucous membrane. This opens into the commencement of the colon and is the termination of the small intestine.

Mucous Membrane of the Small Intestine.—The mucous coat of the small intestine is somewhat thinner than the lining membrane of the stomach. It is thickest in the duodenum and gradually becomes thinner until we reach the ileum. It is highly vascular, presenting, like the mucous membrane of the stomach, a great increase in the quantity of blood during the process of digestion. It has a peculiar soft and velvety appearance, and, during digestion, it is of a vivid-red color, being pale-pink during the intervals. It presents for anatomical description the following parts: 1, folds of the membrane, called valvulæ conniventes; 2, duodenal racemose glands, or the glands of Brunner; 3, intestinal tubules, or follicles of Lieberkühn; 4, intestinal villi; 5, solitary glands, or follicles; 6, agminated glands, or patches of Peyer.

The valvulæ conniventes, simple transverse duplicatures of the mucous membrane of the intestine, are particularly well marked in man, although they are found in some of the inferior animals belonging to the class of mammals, as the elephant and the camel. They render the extent of the mucous membrane much greater than that of the other coats of the intestine. Commencing at about the middle of the duodenum, they extend, with no diminution in number, throughout the jejunum. In the ileum they become progressively more and more scanty, until they are lost at about its lower third. Sappey found about six hundred of these folds in the first half of the small intestine and from two hundred to two hundred and fifty in the lower half. He estimates that, in those portions of intestine where they are most abundant, they increase the length of the mucous membrane to about double that of the tube itself; but in the ileum they do not increase the length more than one-sixth. The folds are always transverse and occupy usually from one-third to one-half of the circumference of the tube, although a few may extend entirely around it. The greatest width of each fold is in the centre, where it measures from a quarter to half an inch. From this the width gradually diminishes until the folds are lost in the membrane as it is attached to the muscular coat. Between the folds are found fibres of connective tissue similar to those which attach the membrane throughout the whole of the alimentary tract. This, though loose, is constant, and it prevents the folds from being effaced, even when the intestine is distended to its utmost. Between the folds are also found blood-vessels, nerves, and lymphatics.

The position and arrangement of the valvulæ conniventes is such that they move freely in both directions and may be applied to the inner surface of the intestine either above or below their line of attachment. It is evident that the food, as it passes along in obedience to the peristaltic movements, must, by insinuating itself beneath the folds and passing over them, be exposed to a greater extent of mucous membrane than if these valves did not exist. This is about the only definite use that can be assigned to them. They cannot, as has been supposed by some, have any considerable influence upon the rapidity of the passage of the alimentary mass along the intestinal canal.

Thickly set beneath the mucous membrane in the first half of the duodenum, and scattered here and there throughout the rest of its extent, are the duodenal racemose glands, or the glands of Brunner. These are not found in other parts of the intestinal canal. In their structure, they closely resemble the racemose glands of the œsophagus. On dissecting the muscular coat from the mucous membrane, they may be seen with the naked eye, in the areolar tissue, in the form of little, rounded bodies, about one-tenth of an inch in diameter. Examined microscopically, these bodies are found to consist of a large number of short, blind tubes branching in every direction and held together by a few fibres of connective tissue. The tubes have blood-vessels ramifying on their exterior and are lined with glandular epithelium. They collect together to terminate in an excretory duct which penetrates the mucous membrane and opens into the intestinal cavity. When these structures are examined in a perfectly fresh preparation, the excretory duct is frequently found to contain a clear, viscid mucus, of an alkaline reaction. This secretion has never been obtained in quantity sufficient to admit of the determination of its chemical or physiological properties. Its quantity must be infinitely small as compared with the secretion produced by the glandular tubes found in such immense numbers throughout the intestinal tract, and it cannot be regarded as constituting an important part of the fluid known as the intestinal juice.

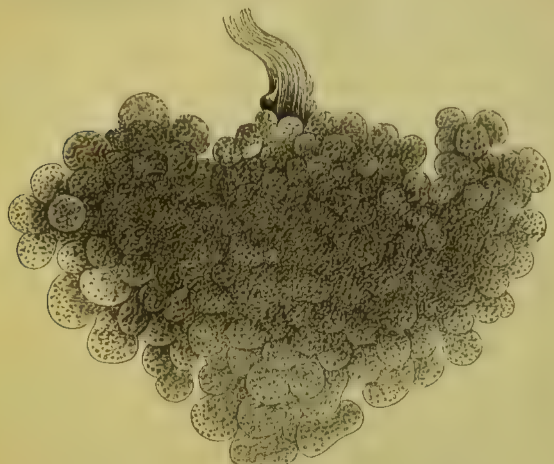


FIG. 64.—*Gland of Brunner, from the human subject.* (Frey.)

The intestinal tubules, or the follicles of Lieberkühn, the most important glandular structures in the intestinal mucous membrane, are found throughout the whole of the small and large intestine. In examining a thin section of the mucous membrane, these little tubes are seen closely packed together, occupying nearly the whole of its structure. From the great extent of the membrane, it can readily be conceived that their number must be immense. Between the tubules, are blood-vessels, embedded in a dense stroma of fibrous tissues with numerous unstriped muscular fibres. In a vertical section of the mucous membrane, the only situations where the tubules are not seen are in that portion of the duodenum where the space is occupied by the ducts of the glands of Brunner and immediately over the centre of the larger solitary glands and some of the closed follicles which are collected to form the patches of Peyer. The tubes are not entirely absent in the patches of Peyer, but are here collected in rings, twenty or thirty tubes deep, which surround each of the closed follicles. A microscopical examination of the surface of the mucous membrane by reflected light shows that the openings of the tubules are between the villi.

The tubules are usually simple, though sometimes bifurcated, are composed externally of a structureless basement-membrane, and are lined with a single layer of columnar epithelium like the cells which cover the villi, the only difference being that, in the tubes, the cells are a little shorter. These cells never contain fatty granules, even during the digestion of fat. The central cavity which the cells enclose, which is about one-fourth of the diameter of the tube, is filled with a clear, viscid fluid, which is the most important constituent of the intestinal juice. The length of the tubules is equal to the thickness of the mucous membrane and is about $\frac{1}{75}$ of an inch. Their diameter is about $\frac{1}{360}$ of an inch. In man, they are cylindrical, terminating in a single, rounded, blind extremity, which is frequently a little larger than the rest of the tube. These tubules are the chief agents concerned in the production of the fluid known as the intestinal juice.

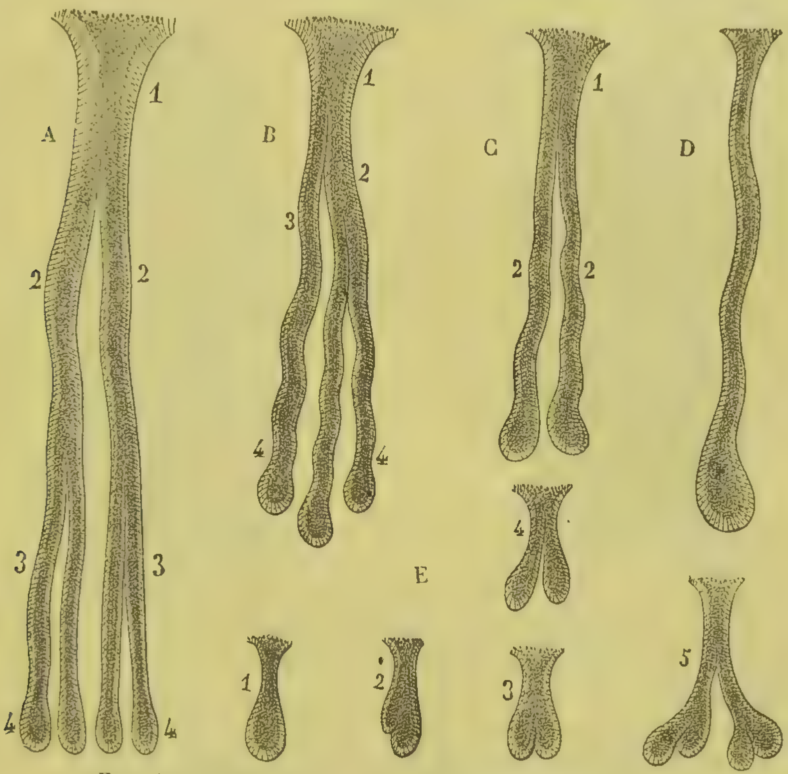


Fig. 65.—*Intestinal tubules; magnified* 100 *diameters.* (Sappey.)

A. From the dog. 1, excretory canal; 2, 2, primary branches; 3, 3, secondary branches; 4, 4, terminal *culs-de-sac.*
B. From the ox. 1, excretory canal; 2, principal branch, dividing into two; 3, branch undivided; 4, 4, terminal *culs-de-sac.*
C. From the sheep. 1, trunk; 2, 2, branches.
D. Single tube, from the pig.
E. From the rabbit and hare. 1, simple gland; 2, 3, 4, bifid glands; 5, compound gland from the duodenum.

The intestinal villi, though chiefly concerned in absorption, are most conveniently considered in this connection. These exist throughout the whole of the small intestine but are not found beyond the ileo-cæcal valve, although they cover that portion of the valve which looks toward the ileum. Their number is very great, and they give to the membrane its peculiar and characteristic velvety appearance. They are found on the valvulæ conniventes as well as on the attached portions of the mucous membrane. In the duodenum and jejunum, they are most numerous. In these parts, there are from fifty to ninety villi to a square line, and, in the ileum, from forty to seventy to a square line. Sappey estimates, on an average, about fifty to the square line and more than ten millions (10,125,000) throughout the whole of the small intestine. The form of the villi varies somewhat in different animals. In the human subject, they are flattened cylinders or cones. In the duodenum, where they resemble somewhat the elevations found in the pyloric portion of the stomach, they are shorter and broader than in other situations and are more like flattened, conical folds. In the jejunum and ileum, they are in the form of long, flattened cones and cylinders. As a rule, the cylindrical form predominates in the lower portion of the intestine. In the jejunum they attain their greatest length, measuring here from $\frac{1}{30}$ to $\frac{1}{20}$ of an inch in length by $\frac{1}{70}$ to $\frac{1}{120}$ of an inch in breadth at their base.

The structure of the villi shows them to be simple elevations of the mucous membrane, provided with blood-vessels, and probably also with lacteals, or intestinal lymphatics. Externally is found a single layer of long, columnar epithelial cells, resting on

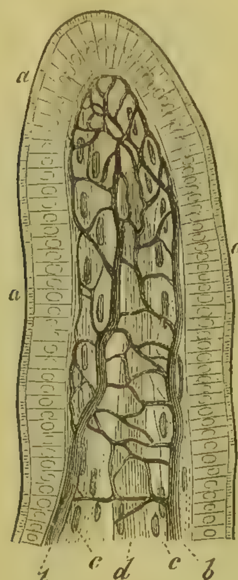


Fig. 66.—*Intestinal villus.* (Leydig.) *a, a, a,* epithelial covering; *b, b,* capillary net-work; *c, c,* longitudinal muscular fibres; *d,* lacteal.

Fig. 67.—*Capillary net-work of an intestinal villus.* (Frey.) *a,* venous trunk; *b,* arterial trunk.

a structureless basement-membrane. These cells, though closely adherent to the subjacent parts during life, are easily detached after death and are almost always destroyed and removed in injected preparations. They adhere firmly to each other and are isolated with difficulty in microscopical preparations. Kölliker has shown that the membranes on the free surfaces of these cells are thickened and finely striated, forming, as it were, a special membrane covering the villus and external to the cells. This membrane may be raised up from the cells and exhibited by the action of water.

Fig. 68.—*Epithelium of the small intestine of the rabbit.* (Funke.)

The substance of the villus is composed of a stroma of amorphous matter, in which are embedded nuclei and a few fibres, fibro-plastic cells, and numerous non-striated muscular fibres. The blood-vessels are very numerous; four or five, and sometimes as many as twelve or fifteen arterioles entering at the base, ramifying through the substance of the villus, but not branching or anastomosing, or even diminishing in caliber until, by a slightly wavy turn or loop, they communicate with the venous radicles, each of which is somewhat larger than the arterioles. The veins all converge to two or three branches, finally emptying into a large trunk situated nearly in the axis of the villus.

The nuclei of the muscular fibres of the villi may be shown by treating them with acetic acid after the epithelium has been removed. These fibres appear to be longitudinal, forming a thin layer surrounding the villus, about half-way between the periphery and the centre and continuous with the muscular coat of the intestine. The muscular fibres, from their arrangement, would seem to be capable of shortening the villus; and this has actually been observed in specimens taken from the intestine shortly after death.

The anatomy of the lacteals as they originate in the villi has been the subject of much controversy; but almost all anatomists are now agreed that these vessels commence by blind extremities, which are either single or present a few short, rounded diverticula leading to a single tube.

Owing to the excessive tenuity of the walls of the lacteals in the villi, it has been found impossible to fill them with an artificial injection, although the lymphatics subjacent to them may be easily distended and studied in this way. Those who profess to have seen the single lacteal in the villus have done so by examining the parts when the lacteal system has been engorged with chyle.

We must still regard the question of the origin of the lacteals in the intestinal villi as one of great obscurity. They may originate by a delicate, anastomosing plexus, just beneath the epithelium, as is thought probable by Sappey, or the chyle may pass through the epithelial layer and a part of the substance of the villus, according to the view presented by Recklinghausen, without the intervention of distinct vessels, until the particles reach the central tube.

No satisfactory account has ever been given of nerves in the intestinal villi. If any exist in these structures, they probably are derived from the sympathetic system, which is largely distributed to the intestinal canal.

The solitary glands or follicles and the patches of Peyer, or agminated glands, have one and the same structure, the only difference being that those called solitary are scattered singly in very variable numbers throughout the small and large intestine, while the agminated glands consist of numbers of these follicles collected into patches of different sizes. These patches are generally found in the ileum. The number of the solitary glands is so variable that it is impossible to give any general estimate of it. They are sometimes absent. The patches of Peyer are always situated in that portion of the intestine opposite the attachment of the mesentery. They are likewise variable in number and are irregular in size. They usually are irregularly-oval in form, and measure from half an inch to an inch and a half in length by three-fourths of an inch in breadth. Sometimes they are three or four inches long, but the largest are always found in the lower part of the ileum. Their number is about twenty, and they are generally confined to the ileum; but when they are very numerous—for they sometimes exist to the number of sixty or eighty—they may be found in the jejunum or even in the duodenum.

Two varieties of the patches of Peyer have been lately described by anatomists. In one of these varieties, the patch is quite prominent, its surface being slightly raised above the general mucous surface, while, in the other, the surface is smooth, and the patch is distinguished at first with some difficulty. The more prominent patches are covered with mucous membrane arranged in folds something like the convolutions on the surface of the brain. The valvulæ conniventes are arrested at or very near their borders. These are the only patches which are generally described as the glands of Peyer, the others, which may be called the smooth patches, being generally overlooked. The latter are covered with a smooth, thin, and closely-adherent mucous membrane. Their follicles are small and numerous. The borders of these patches are much less strongly marked than those of the first variety. As they are evident only upon close examination and as they are the only patches present in certain individuals, it is said that sometimes the patches of Peyer are entirely wanting. They are generally less numerous than the first variety and, according to Sappey, are most abundant in persons of feeble constitution. The villi are very large and prominent on the mucous membrane covering the first variety of Peyer's patches, especially at the summit of the folds. In the second variety, the villi are the same as over other parts of the mucous membrane, except that they are placed more irregularly and are not so numerous.

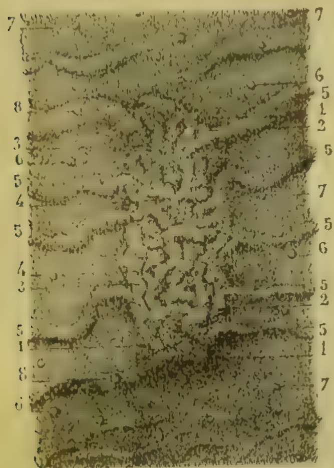


FIG. 69.—*Patch of Peyer.* (Sappey.)
1, 1, 1, patch of Peyer; 2, 2, folds seen on the surface; 3, 3, grooves between the folds; 4, 4, fossettes between some of the folds; 5, 5, 5, 5, 5, 5, 5, 5, valvulæ conniventes; 6, 6, 6, 6, solitary glands; 7, 7, 7, 7, smaller solitary glands; 8, 8, solitary glands upon the valvulæ conniventes.

The intimate structure of the patches of Peyer has not been definitely settled in all its particulars. It is well determined, however, that the follicles which compose them are completely closed, the openings which have been said to exist being undoubtedly accidental ruptures made in preparing specimens for microscopical examination. These follicles are somewhat pear-shaped, with their pointed projections directed toward the cavity of the intestine. Just above the follicle, there is generally a small opening in the mucous membrane, surrounded by a ring of intestinal tubules, and leading to a cavity, the base of which is convex and formed by the conical projection of the follicle. The diameter of the follicles is from $\frac{1}{72}$ to $\frac{1}{24}$ or even $\frac{1}{12}$ of an inch. The small-sized follicles are generally covered by mucous membrane and have no opening leading to them. Each follicle consists of a rather strong capsule composed of an almost homogeneous or very slightly fibrous membrane, enclosing a semifluid, grayish substance, cells, blood-vessels, and probably lymphatics. The semifluid matter is of an albuminoid character. The cells are very small, rounded, and mingled with numerous small, free nuclei. The blood-vessels have rather a peculiar arrangement. In the first place they are distributed between the follicles, so as to form a rich net-work surrounding each one. Numerous capillary branches are sent from these vessels into the interior of the follicle, returning in the form of loops. The obscurity in the anatomy of the follicles is chiefly with regard to the arrangement of their lymphatic vessels. These have not been distinctly traced within the investing membrane. They have been demonstrated surrounding the follicles, but it is still doubtful whether they exist in their interior. This question is so unsettled that it is impossible to make a definite statement on the subject. All that is known is that, during digestion, the number of lacteals coming from the Peyerian patches is greater than in other parts of the mucous membrane; but vessels containing a milky fluid are never seen within the follicles.

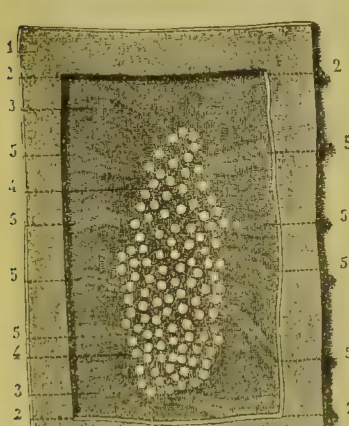


FIG. 70.—*Patch of Peyer, seen from its attached surface.* (Sappey.)
1, 1, serous coat of the intestine; 2, 2, 2, 2, serous coat removed to show the patch; 3, 3, fibrous coat of the intestine; 4, 4, patch; 5, 5, 5, 5, 5, 5, 5, 5, valvulæ conniventes.

The mucous membrane covering the prominent patches is generally so thick and folded that the closed follicles cannot be seen from above and are only discernible from the under surface. In the smooth patches, the follicles are generally well brought out by maceration in acetic acid.

The description of the follicles which compose the patches of Peyer answers, in general terms, for the solitary glands, except that the latter are found in both the small and the large intestine.

Intestinal Juice.

Of the three fluids with which the food is brought in contact in the intestinal canal, namely, the bile, the pancreatic juice, and the intestinal juice, the last, the secretion of the mucous membrane of the small intestine, presents the greatest difficulties in the investigation of its properties and function. If it be admissible to reason from the known mechanism of secretion in other parts, it is fair to suppose that the normal secretion from the mucous membrane of the small intestine can only take place in obedience to the stimulus of food. The same cause induces the secretion of the pancreatic juice and increases the flow of bile. As we have already seen, the food, as it passes from the stomach into the duodenum, is to a great extent disintegrated and is mingled with the secretions from both the mouth and the stomach. Under these circumstances, it is evidently impossible to collect the intestinal juice under perfectly physiological conditions, in a state of purity sufficient to allow of extended experiments regarding its composition, properties, and action in digestion.

Bidder and Schmidt experimented upon dogs and cats, shutting off from the intestine the bile and pancreatic juice, and found that starch introduced into the canal became transformed into sugar. They also observed that fat was emulsified to a considerable degree, and that albumen and meat were partially disintegrated and digested. These observers were unable to collect the intestinal juice in quantity sufficient for analysis. That which they obtained was found to be colorless, very viscid, and strongly alkaline in its reaction.

As far as the composition and general properties of the intestinal juice are concerned, the observations of Colin upon horses are the most definite, although it is questionable whether he succeeded in obtaining the fluid in a normal state. To collect the fluid, an incision was made into the abdominal cavity, and from four and a half to six feet of the small intestine were drawn out. This portion was emptied by gently pressing with the finger from above downward, while, with the other hand, the upper portion was kept closed. Without removing the fingers, two soft clamps were then applied, thus shutting off the exposed part of the intestine from the rest of the canal. The gut was then returned and the wound in the abdomen closed. At the end of half an hour, the animal was killed by bleeding, and the contents of the isolated portion of the intestine were examined. The quantity of juice obtained was considerable, being from 1,235 to 1,852 grains for about six and a half feet of intestine. It was always found to be much less when intestinal digestion had been suspended, and its quantity could be increased by the injection into the loop of a little solution of manna, sulphate of soda, or aloes. The fluid thus obtained was clear, slightly yellowish, with a saline taste and an alkaline reaction. It was mixed with mucus, which formed a sediment when the fluid was allowed to stand, and could be separated by filtration. Notwithstanding the care with which these observations were conducted, it is not probable that the fluid thus obtained by Colin was the normal intestinal juice; and it certainly does not correspond in its general characters with the fluids which have been studied by other experimenters.

FIG. 71.—*Clamp for isolating a portion of the intestine.* (Colin.) *A*, lower plate; *B*, upper plate; *C*, fixed screw; *D*, movable screw in place; *E*, screw turned so as to allow the clamp to be passed around the intestine.

It becomes an interesting question, in this connection, to determine whether the solitary and the agminated glands produce any secretion which is discharged into the intestinal cavity. Although these follicles are closed, the observations of Colin have shown pretty conclusively that they are capable of producing a secretion; but the precise mode of its formation is not so apparent. The experiment by which this was demonstrated was made on a pig, an animal in which there is an enormous agminate gland, ribbon-shaped and over six feet in length. That portion of the ileum in which the gland is situated was emptied, and about four and a half feet of it were isolated by two ligatures from the rest of the canal. At the end of an hour the animal was killed and the intestine examined. The surface of the gland was found covered with a layer of mucus, thicker and more consistent than over other portions of the membrane. The only way in which it could reasonably be supposed that this secretion was produced is by exhalation through the membranes of the follicles, as there is no evidence that their contents are discharged by rupture.

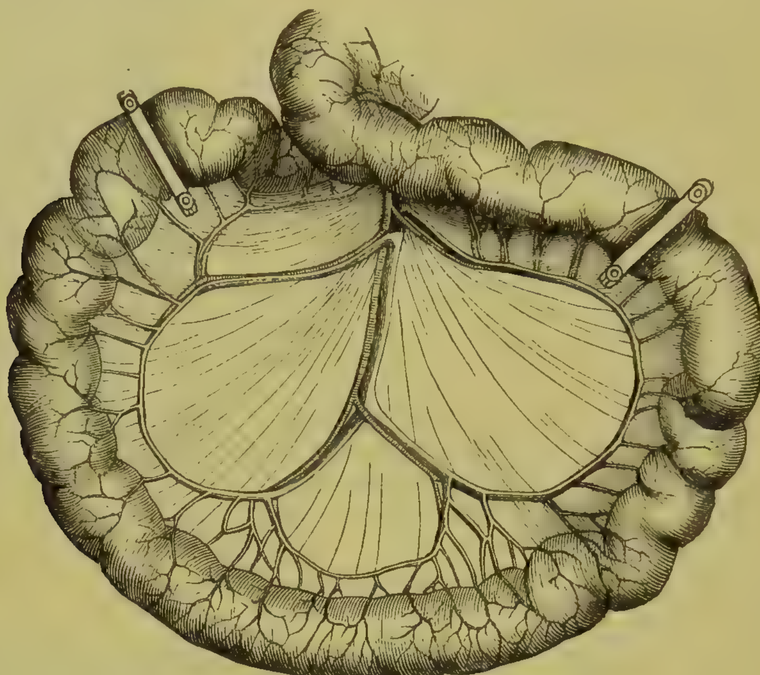


FIG. 72.—*Isolated portion of the intestine.* (Colin.)

Taking only into consideration experiments upon the inferior animals, little definite information has been obtained concerning the composition and properties of the intestinal juice. We can readily see that this must be the case, since it has thus far been impossible, in observations of this kind, to fulfil the necessary physiological conditions. Farther facts are evidently needed to harmonize the opposite results arrived at by different experimenters. It was the same in the progress of the physiology of stomach-digestion, which was unsettled and obscure until the normal gastric juice was obtained by Beaumont. The following case of intestinal fistula, reported by Busch, has done much to elucidate this subject:

The case referred to was that of a woman, thirty-one years of age, who, in the sixth month of her fourth pregnancy, was injured in the abdomen by being tossed by a bull. The wound was between the umbilicus and the pubes, presenting two contiguous openings connected with the intestinal canal. It was supposed that the openings were into the upper third of the small intestine. At the time the patient first came under observation, every thing that was taken into the stomach was discharged by the upper opening, and all attempts to establish a communication between the two by a surgical operation had failed. At this time, the patient was extremely emaciated, had a voracious appetite, and was evidently suffering from defective nutrition resulting from the constant discharge of alimentary matter from the fistula. Having been treated, however, by the introduction of cooked alimentary substances into the opening connected with the lower end of the intestine, she soon improved in her nutrition and was then made the subject of extended and interesting observations upon intestinal digestion.

With regard to the general properties of the intestinal juice, the observations of Busch upon his case of intestinal fistula agree with those of Bidder and Schmidt upon the lower animals. He never, in the natural condition, found a large quantity of secretion in the intestine. The fluid was white or of a pale rose-color, consistent, and always strongly alkaline. The maximum proportion of solid matter which it contained was 7·4 and the minimum, 3·87 per cent. The secretion apparently could not be obtained in sufficient quantity for ultimate analysis. No better opportunity than this could be presented for studying the intestinal juice in its pure state. The nature of the case made it impossible that there should be any admixture of food, pancreatic juice, bile, or the secretion of the duodenal glands; and, during the process of digestion, the lower part of the intestine undoubtedly produced a fluid of perfectly normal character. When we come to consider the action of the intestinal juice upon the various articles of food, our most reliable facts will be drawn from the observations made upon this case.

From what has been ascertained by experiments upon the lower animals and observations on the human subject, the intestinal juice has been shown to possess the following characters:

Its quantity in any portion of the mucous membrane which can be examined is small; but, when the extent of the canal is considered, it is evident that the entire quantity of intestinal juice must be great, although, beyond this, no reliable estimate can be made.

The intestinal juice is viscid and has a tendency to adhere to the mucous membrane. It is generally either colorless or of a faint rose-tint, and its reaction is invariably alkaline.

With regard to the composition of the intestinal juice, little of a definite character has been learned. All that can be said is that its solid constituents exist in the proportion of about 5·47 parts per hundred. In most analyses of fluids from the intestine, there is reason to believe that the normal intestinal juice was not obtained.

The organs which secrete the fluid known as the intestinal juice are the follicles of Lieberkühn, the glands of Brunner, and possibly the solitary follicles and patches of Peyer. The fluid, however, is chiefly secreted by the follicles of Lieberkühn, which, as we have seen, exist in the mucous membrane of the intestine in immense numbers. Although the other organs mentioned do not contribute much to the secretion, they produce a certain quantity of fluid; and the intestinal juice must be regarded as a compound fluid, like the saliva, and not the product of a single variety of glands, like the gastric juice.

Action of the Intestinal Juice in Digestion.

The physiological action of the intestinal juice has been closely studied in the inferior animals by Frerichs and by Bidder and Schmidt, but their experiments have been somewhat contradictory. All observers, however, are agreed that this fluid is more or less active in transforming starch into sugar. We must turn finally to the observations of Busch, on the case of intestinal fistula in the human subject, for the most satisfactory and definite information on this subject. In many points, it is true, these observations simply confirm those which have been made upon the inferior animals, but they are of great value, as they establish conclusively many important facts regarding the physiological action of the intestinal juice in the human subject.

In the case reported by Busch, starch, both raw and hydrated, when introduced into the lower opening, where it came in contact only with the intestinal juice, was invariably changed into glucose. Cane-sugar was not transformed into glucose but appeared in the fæces as cane-sugar. This is important, with reference both to the want of action of the intestinal juice upon cane-sugar and the fact that cane-sugar, as such, is not absorbed in quantity by the intestinal mucous membrane.

Coagulated albumen and cooked meat were always more or less digested by the intestinal juice. This fact coincides with the observations of Bidder and Schmidt.

The observations which were made on fats, melted butter, and cod-liver oil, showed that the pure intestinal juice had little or no action upon them. These substances always appeared in the fæces unchanged. When, however, fatter matters were taken into the stomach, they were discharged from the upper opening in the intestine, in the form of a very fine emulsion, and could not be recognized as fat.

It is evident, from these facts, that the intestinal juice is important in digestion, more as a fluid which aids the general process as it takes place in the small intestine than as one which has a peculiar action upon any distinct class or classes of alimentary principles. It undoubtedly assists in completing the digestion of albuminoid substances and in transforming starch into sugar. Although, in the latter process, its action is very marked, the same property belongs to the saliva and the pancreatic juice. Intimately mingled—as it always is during digestion—with the bile and the pancreatic juice as well as with various alimentary substances, the intestinal juice should be studied as it operates upon the food, in connection with the other fluids found in the small intestine, the digestive action of all being most intimately associated.

Pancreatic Juice.

The physiological anatomy of the pancreas does not demand a very extended consideration, as most of the points of its descriptive anatomy have no direct relation to its physiology, and its minute anatomy belongs properly to the subject of secretion. The pancreas is a glandular organ, situated transversely in the upper part of the abdominal cavity, and closely applied to its posterior wall. Its form is elongated, with an enlarged, thick portion, called the head (which is attached to the duodenum), a body, and a pointed extremity, which is in close relation to the hilum of the spleen. Its average weight is from four to five ounces; its length is about seven inches; its greatest breadth, about an inch and a half; and its thickness, three-quarters of an inch. It lies behind the peritoneum, which covers only its anterior surface.

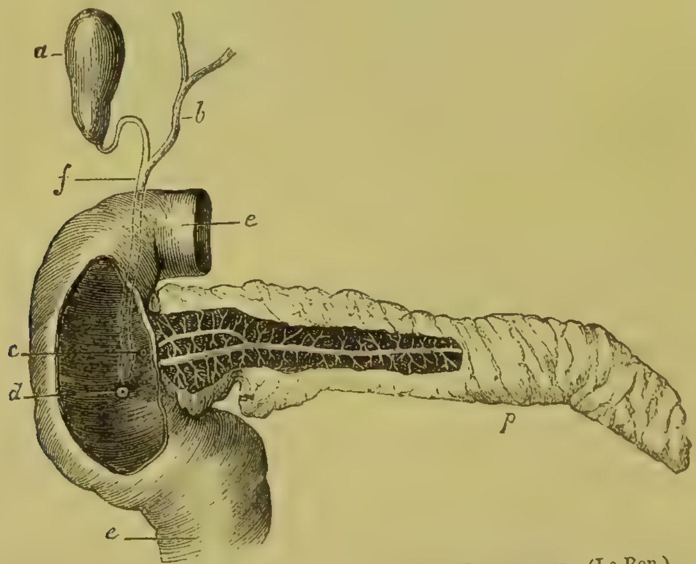


FIG. 73.—*Gall-bladder, ductus choledochus, and pancreas.* (Le Bon.)
a, gall-bladder; *b*, hepatic duct; *c*, opening of the second duct of the pancreas; *d*, opening of the pancreatic and the bile-duct; *e*, *e*, duodenum; *f*, ductus choledochus; *p*, pancreas.

According to Bernard, who has made numerous investigations into the anatomy of this gland, there are nearly always, in the human subject, two ducts opening into the duodenum; one which opens in common with the ductus communis choledochus, and one which opens about an inch above the main duct, called by Bernard the recurrent or accessory duct. The main duct is about an eighth of an inch in diameter and extends along the body of the gland, becoming larger as it approaches the opening. The second duct is smaller and becomes diminished in caliber as it nears the duodenum. Many anatomists describe but a single duct, regarding the other as anomalous. The dissections of Bernard, however, were very numerous and show the almost constant occurrence of two ducts.

In general appearance and minute structure, the pancreas is like the parotid and submaxillary glands. By the older anatomists it was known as the "abdominal salivary gland," on account of this resemblance in structure and an assumed similarity in the nature of their secretions. Recent developments in the physiology of the pancreatic juice have caused this name to be discarded.

Bernard was the first to obtain normal pancreatic juice from a living animal and to give a definite idea of its properties and functions; a point which it is proper to particularly insist upon, inasmuch as, since his discovery, some have pretended that the facts which he established had been demonstrated before. The following method for collecting the pancreatic juice from a living animal, one which we have repeatedly employed with success, is essentially that recommended by Bernard:

The animal generally employed by Bernard in these experiments is the dog. Selecting one of tolerably large size, he is secured to the operating-table and placed upon his left side. An incision from three to four inches in length is then made in the right hypochondrium, just below and parallel with the border of the last rib. The parts are first divided down to the fascia transversalis and the peritoneum. An opening is then made into the abdominal cavity about half the length of the incision through the skin and muscles, which brings to view the duodenum and a portion of the pancreas. The duodenum, with the pancreas attached to it, is then carefully drawn out of the abdomen. The next step is to introduce a small canula into the principal pancreatic duct. In the dog, there are always two pancreatic ducts; a small duct, which opens into the intestine at or near the opening of the bile-duct, and a principal duct, which is situated about an inch below. To collect the juice, the tube should be introduced into the principal duct. This is found by turning the duodenum and pancreas so as to expose the posterior surface of the gland, when the duct, which is very short and almost concealed by the tissue of the pancreas, may be seen obliquely penetrating the intestinal wall. In the dog, the pancreas is composed of two portions; one, called the horizontal portion, which is attached to the duodenum, and a vertical portion, which passes away from the intestine between the folds of the mesentery. The duct is generally situated near the point where the pancreas ceases to be attached to the intestine. The tissue of the pancreas is to be carefully pushed away from the duct with the end of the canula or the point of a knife, a small longitudinal slit is made in it with the scissors, and a silver canula, about one-twelfth of an inch in diameter and four inches in length, is introduced and firmly secured in place by a ligature which has previously been

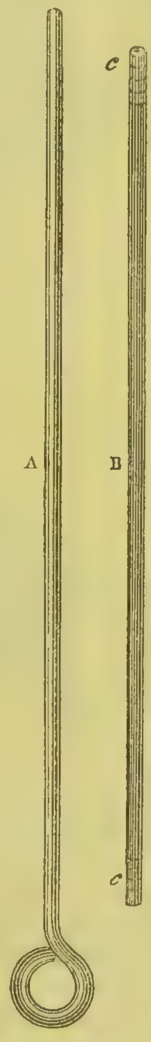


FIG. 74.—*Canula for a pancreatic fistula.* (Bernard.)

A, stylet, the extremity of which should pass a little beyond the end of the canula B, to facilitate its introduction into the pancreatic duct; B, canula, provided with little grooves c, c, to hold the threads for attachment into the duct and into the bladder used to collect the pancreatic juice.

thrown around the duct. The canula should be provided with a well-fitting stylet, with the point rounded so that it may be introduced into the duct with ease; and the end of the canula should be somewhat roughened, so that the ligature may secure it well in place. The canula will enter the duct for a short distance only, and it should not be introduced forcibly. After this has been accomplished, the canula may be steadied by attaching it with a single stitch to the wall of the intestine. The stylet is now to be withdrawn and the parts carefully returned to the abdomen, leaving the end of the canula projecting at the anterior portion of the wound, which should be carefully closed. Bernard recommends to first raise up the fascia and peritoneum with hooks and carefully attach their edges with sutures, and then to close, in the same way, the incision in the muscles and integument. The animal may now be kept upon the table, and the fluid which is discharged from the tube collected in a test-tube, or a thin gum-elastic-bag may be attached. This may be provided with a stopcock, so that the fluid may be drawn off at will.

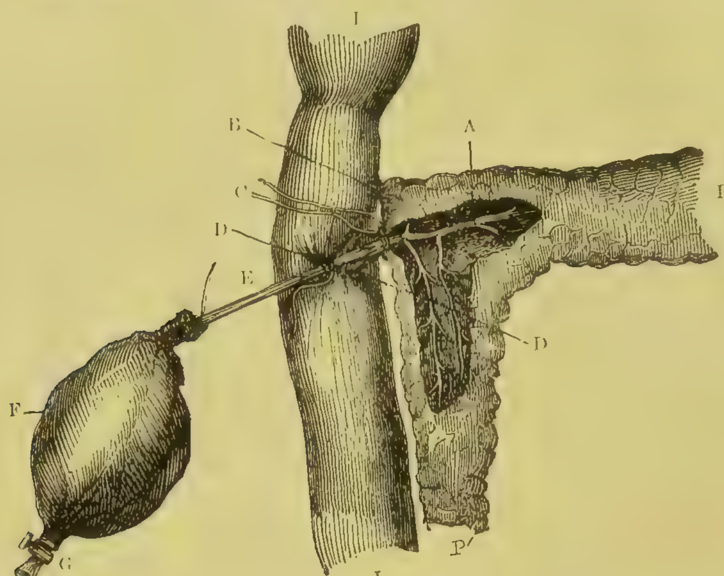


FIG. 75.—*Canula fixed in the pancreatic duct.* (Bernard.)

A, principal pancreatic duct of the dog; B, smaller pancreatic duct; C, ligature securing a canula in the principal duct; D, D, ligature attaching the canula to the intestine, for security; E, canula; F, bladder, provided with a stopcock G, to collect the pancreatic juice; P, P, pancreas; I, I, intestine.

Like the other digestive fluids, the pancreatic juice is secreted in abundance only during the process of digestion. It is therefore necessary to feed the animal moderately about an hour before the operation, so that the pancreas may be in full activity. When it is exposed at that time, it is filled with blood and has a rosy tint, contrasting strongly with its pale appearance during the intervals of digestion.

In performing the above experiment, it is generally better not to employ an anæsthetic agent, as this very frequently produces vomiting, arrests digestion for a time, and consequently interferes with the secretion of the pancreatic juice. This, however, is not always the case. We have sometimes performed the operation with the aid of ether and have obtained a fair amount of fluid. It is also necessary to avoid traction upon the duodenum as much as possible, for this is almost sure to produce vomiting. To obtain the best results, the operation should be performed rapidly and with very little exposure of the pancreas. In some very successful experiments, Bernard has obtained from sixty to one hundred grains of juice in an hour, from a dog of medium size.

Some of the most interesting facts developed by Bernard concerning the pancreatic juice relate to phenomena connected with its secretion. It is important to remember that the secretion of the pancreas is entirely suspended during the intervals of digestion. This fact has been definitely settled by Bernard and can easily be observed by opening animals in digestion and while fasting. In the first instance, the pancreatic duct will be found full of normal secretion, and, in the other, it will be almost, if not entirely, empty. Bernard has also found that the pancreatic juice begins to flow into the duodenum during the first periods of stomach-digestion, before alimentary matters have begun to pass in quantity into the intestine.

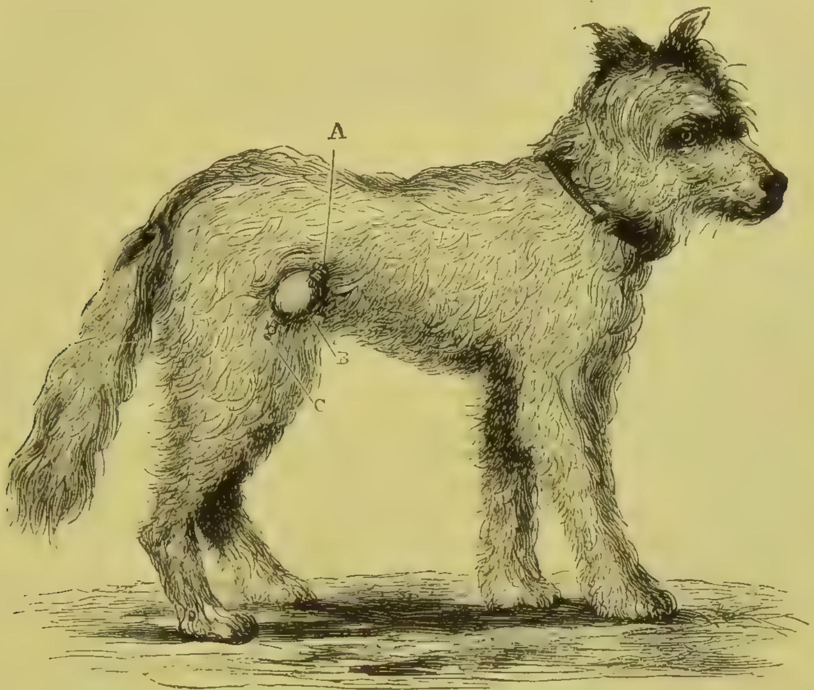


Fig. 76.—*Pancreatic fistula.* (Bernard.)

Full-grown shepherd-dog (female), in which a pancreatic fistula has been established. A, silver tube to which a bladder has been attached; B, bladder; C, stopcock for the purpose of collecting the juice which accumulates in the bladder.

Another important fact determined by Bernard is that the secretion of the pancreas is readily modified by irritation and inflammation following the operation. When we come to treat of the general properties of the normal pancreatic fluid, it will be seen that its characteristics are, decided alkalinity, viscid consistence, and coagulability by heat. It is almost always the case that, a few hours after the canula is fixed in the duct, the juice loses some of these characters and flows in abnormal quantity. With respect to susceptibility to irritation, the pancreas is peculiar; and its secretion is sometimes abnormal from the first moments of the experiment, especially if the operative procedure have been prolonged and difficult. That the properties above described are characteristic of the normal pancreatic secretion, there can be no doubt; as, in all instances, fluid taken from the pancreatic duct of an animal suddenly killed while in full digestion is strongly alkaline, viscid, and coagulable by heat. This excessive sensitiveness of the pancreas has rendered fruitless all the attempts of Bernard to establish a permanent pancreatic fistula from which the normal juice could be collected; and we are not disposed to admit that the fluid collected by recent German observers, from permanent fistulæ, represents physiological conditions.

General Properties and Composition of the Pancreatic Juice.—In all the inferior animals from which the pancreatic secretion has been obtained in a normal condition, the fluid has been found to present pretty uniform characters. It is viscid, slightly opaline, and has a distinctly alkaline reaction. Bernard found the specific gravity of the fluid from the dog to be 1040. The quantity of organic matter which the normal secretion contains is very great, so that the fluid is completely solidified on the application of heat. This great coagulability is one of the properties by which the normal fluid may be distinguished from that which has undergone alteration.

Composition of the Pancreatic Juice of the Dog. (Bernard.)

Water	900 to	920
Organic matter, precipitable by alcohol and containing always a little lime (pancreatine)	90 to	73·60
Carbonate of soda, Chloride of sodium, Chloride of potassium, Phosphate of lime,	10 to	6·40
	1,000	1,000

Most of the analyses which have been made of the pancreatic fluid are not to be relied upon, as the manner in which the juice was obtained shows generally that it was not normal. There is no doubt, however, that the fluid which was obtained from the dog and analyzed by Bernard possessed all of its characteristic physiological properties.

The chemical properties of the organic principle of the pancreatic juice are distinctive. Although, like albumen, it is coagulated by heat, the strong mineral acids, and absolute alcohol, it differs from albumen in the fact that its dried alcoholic precipitate can be re-dissolved in water, giving to the solution all the physiological properties of the normal pancreatic secretion. Bernard has also found that pancreatine is coagulated by an excess of sulphate of magnesia, which will coagulate caseine but has no effect upon albumen. It is important to recognize this distinction between pancreatine and other nitrogenized principles, especially albumen, from the fact that the last-named substance has the property of forming an emulsion with fats, though not so readily and completely as the pancreatic juice; and it is essential to decide whether the organic principle be a peculiar and distinct substance, or albumen transuded pathologically, perhaps, from the blood. There can be no doubt, in view of the marked chemical and physiological peculiarities of pancreatine, that this is a distinct proximate principle, which is characteristic of the pancreatic secretion and found in no other fluid.

Researches have shown that pancreatine is the essential physiological constituent of the pancreatic juice and the only one which gives this fluid its peculiar digestive properties. The contents of the duodenum, as the partly digested matters pass from the stomach, are generally acid; but this does not at all interfere with the action of the pancreatic juice. Although the secretion itself is alkaline, it retains its physiological properties when it has been rendered acid by admixture with gastric juice.

The inorganic constituents of the pancreatic juice do not possess any great physiological interest, inasmuch as they do not seem to be essential to its peculiar digestive properties. It has been shown, indeed, by Bernard, that the organic principle alone, extracted from the pancreatic juice and dissolved in water, is capable of imparting to the fluid all the physiological characters of the normal secretion.

The entire quantity of pancreatic juice secreted in the twenty-four hours has been variously estimated by different authors. After what has been said concerning the variations to which the secretion is subject, it is not surprising that these estimates should present great differences. Bernard was able to collect from a dog of medium size from eighty to one hundred grains in an hour; but it must be remembered that only one of the ducts was operated upon, and that the gland is always very susceptible to irritation. There is no accurate basis for an estimate of the quantity of pancreatic fluid secreted in the twenty-four hours in the human subject, or of the quantity necessary for the digestion of a definite amount of food.

Unlike the gastric juice, the secretion of the pancreas, under ordinary conditions of heat and moisture, rapidly undergoes decomposition. In warm and stormy weather, the alteration is marked in a few hours; but, at a temperature of from 50° to 70° Fahr., it decomposes gradually in from two to three days. The changes which the fluid thus undergoes are interesting, from the fact that some physiologists, having experimented with an altered or an abnormal secretion, have failed to recognize certain of the characteristic properties of the normal fluid. As it thus undergoes decomposition, the fluid acquires a very offensive, putrefactive odor, and its coagulability diminishes, until finally it is not affected by heat. The alkalinity, however, increases in intensity; and, when neutralized with an acid, there is a considerable evolution of carbonic acid, which does not occur in fresh pancreatic juice.

Action of the Pancreatic Juice in Digestion.

It is only since the observations of Bernard, in 1848, that the pancreatic juice has been regarded as a fluid of any great importance in digestion. It has now been demonstrated, both by cases of disorganization of the pancreas in man and by experiments on animals in which the tissue of the organ has been destroyed, that the pancreatic juice is essential to digestion and to life, animals dying of inanition when its function has been abolished.

The most striking feature in the discovery made by Bernard was the action of the pancreatic juice in the digestion of fats; it being shown that these principles are acted upon almost exclusively by the pancreas, and that they pass through the alimentary canal undigested when this organ has been destroyed. For this reason, probably, the action of the pancreas in the digestion of fatty substances has received an undue prominence; and its action upon other articles of food, though not at the present day overlooked, does not always receive proper consideration. We shall find that the pancreatic juice has an important action in the digestion of nearly all the alimentary principles as they pass out from the stomach.

Action upon Fats.—Even before the publication of Bernard's researches, it was pretty generally admitted that the digestion of fat consisted in its minute subdivision and suspension in the form of an emulsion. This view was adopted from the fact that, during the absorption of fats from the intestinal canal, the lacteals and thoracic duct always contain innumerable small, fatty globules; but the ideas of physiologists as to the particular fluid by which the emulsification of fats is accomplished were not very well settled. The most generally-received opinion, however, was that this was effected by the bile; but experiments on this subject were very contradictory.

One of the most remarkable facts observed by Bernard was that, in the rabbit, after the ingestion of fatty matters, vessels filled with white chyle do not make their appearance at the commencement of the small intestine, as in other animals, but are first seen from twelve to twenty inches below the pylorus. The anatomical peculiarity in these animals is that the pancreatic duct, instead of opening into the intestine with the bile-duct at the upper part of the small intestine, has its opening from twelve or twenty inches below, just at the point where the chyliferous vessels are observed. This fact, which we have frequently confirmed, points directly to the pancreatic juice as the agent principally, if not exclusively, concerned in emulsifying the fats; while it shows that the bile possesses little or no immediate efficiency in this regard. Following out this line of inquiry, and operating with fresh, coagulable pancreatic juice and the liquid fats or those capable of being liquefied by gentle heat, it was found that slight agitation of this fluid with the fats produced a very fine and permanent emulsion, similar in every respect to the milky fluid found in the lacteals during digestion. In fact, comparative analyses of the lymph and chyle have shown that the latter liquid is nothing more than lymph with the addition of fatty emulsion. As soon as the absorption of fat is completed, the lacteal vessels lose their opaque, white contents and carry nothing but colorless lymph. This is one of the great experimental facts upon which is based the view that the pancreatic juice has the property of digesting the fats. Concerning the accuracy of this observation there can be no doubt. The fact has been so frequently confirmed, that it must now be considered as established beyond question, and we can add our testimony to its accuracy from personal observation. It is true that some of the German physiologists have been unable to confirm these experiments; but, by carefully following out the process indicated by Bernard, which is detailed with great care, we have invariably found his observations to be correct. It is well known that many of the German experimenters operated with pancreatic juice which was not coagulable and which Bernard regards as abnormal and incapable of digesting fat.

The pancreatic juice is the only one of the digestive fluids which is capable of forming a complete and permanent emulsion with fats. The fact that the other digestive fluids will not accomplish this is easily demonstrated as regards the saliva, gastric juice, and bile. The intestinal juice is then the only one which might be supposed to have this property. The observations of Busch on this point, in his case of intestinal fistula, are conclusive. He found that fatty matters taken into the stomach were discharged from the upper opening in the intestine in the form of a fine emulsion and were never recognizable as oil; but that fat introduced into the lower intestinal opening was not acted upon and was discharged unchanged in the fæces.

Another peculiarity noted by Bernard in the emulsion resulting from the action of pancreatic juice upon fats is that it persists when diluted with water and will pass through a moistened filter like milk. This does not take place in the imperfect emulsion formed by a mixture of oil with any other of the digestive fluids.

Although the normal pancreatic juice is constantly alkaline, this is not an indispensable condition as regards its peculiar action upon fats; for the emulsion is none the less complete when the fluid has been previously neutralized with gastric juice.

Bernard has shown that the pancreatic juice and the tissue of the pancreas have the property of saponifying fats, or decomposing them into a fatty acid and glycerine, and that this property is not possessed by any other tissue or liquid of the economy. The question naturally arises, then, whether this be an accidental property of the tissue and the secretion of the pancreas or whether partial saponification of fat take place in digestion. Concerning this point there is no difference of opinion among physiological chemists. The fat which is contained in the lacteal vessels is always neutral; and the absence of any fatty acid has been recognized by Bernard as well as by others. The inevitable conclusion to be drawn from this fact is, that, while fat may be in part decomposed into an acid and glycerine by the pancreatic juice, out of the body, in the natural process of digestion, either this does not take place or the acid is not absorbed by the lacteals. The greatest part, if not the whole, of the fat which is digested in the small intestine is simply formed into an emulsion by the pancreatic juice and undergoes no chemical alteration.

To complete the experimental evidence of the action of the pancreatic juice in the digestion of fats, Bernard attempted to extirpate or destroy the pancreas in a living animal. This he found very difficult. All attempts to extirpate the organ with the knife being unsuccessful, the injection of foreign matters into the duct was resorted to. After a great number of unsuccessful experiments, in two instances, the functions of the gland were suspended for a time and its tissue was partly destroyed by the injection of melted tallow. In both of these observations, the effects upon digestion were very marked. Although the appetite was voracious, the animals became gradually emaciated, and the fæces contained a large quantity of rancid, undigested fat. At the same time, other alimentary principles, incompletely digested, were recognized in the discharges. In two dogs operated upon by Bernard, in which the experiments were successful, the nutrition and the alvine discharges became normal at the thirteenth and the seventeenth day. After the animals had completely recovered, they were killed, and the pancreas in both instances was found partially destroyed.

Now that the action of the pancreatic juice upon fats is so well understood, it is a matter of surprise that the cases of fatty diarrhœa connected with disorganization of the pancreas, which were reported by Dr. Richard Bright, in 1832, did not direct the attention of physiologists to the function of this organ. These cases, with others of a similar character which have been reported from time to time, are now brought forward as strong evidence of the action of the pancreas in the digestion of fats. Many of them presented a train of symptoms analogous to those observed in animals after partial destruction of the gland. The presence of fat in the alvine dejections was most marked; and, as is now well known, this could be nothing but the undigested fatty principles of the food. In the three cases observed by Bright, the pancreas was found so disorganized that its secreting function must have been almost, if not entirely, abolished. In the case reported by Mr. Lloyd, the condition was the same; and, in the case reported by Dr. Elliotson, "the pancreatic duct and the larger lateral branches were filled with white calculi." Another interesting case of disease of the pancreas is described in the catalogue of the Anatomical Museum of the Boston Society for Medical Improvement, in 1847. In this case, it was observed by the patient that fatty discharges from the bowels did not take place unless fatty articles of food had been taken. After death, a large tumor was found in the situation of the pancreas, but all trace of the normal structure of the organ had been destroyed. Many more cases of this character are quoted by Bernard and others, and they fully confirm the observations and experiments which have been made upon the lower animals. They all seem to show that the function of the pancreas in digestion is essential to life, but that one of the chief disorders in digestion incident to the destruction of this gland relates to the digestion of fats.

Taking into consideration all the facts bearing upon this subject, the conclusion is inevitable that the chief agent in the digestion of fats is the pancreatic juice; and that this fluid acts by forming with the fat a very fine emulsion, thus reducing it to a form in which it can be absorbed. How far the bile may assist in this process is a question which will come up for consideration hereafter; but the facts with regard to the pancreatic juice are conclusive.

Action upon Starchy and Saccharine Principles.—All physiologists are agreed with regard to the action of the pancreatic juice in transforming starch into sugar. This was first observed, in 1844, by Valentin, who experimented with an artificial fluid made by infusing pieces of the pancreas in water. Bouchardat and Sandras first noted this property in the normal pancreatic secretion.

The property of converting starch into sugar is possessed by several of the digestive fluids. We have seen that the starchy elements of food are acted upon by the saliva, that this action is not necessarily arrested as these principles, mixed with the saliva, pass into the stomach, and that the intestinal juice of itself is capable of effecting the transformation of starch into sugar to a considerable extent. It therefore becomes an important question to determine precisely how far the pancreas is actually concerned in the digestion of this class of principles.

Bernard places the pancreatic juice at the head of the list of the digestive fluids which act upon starch. This view is undoubtedly correct; although he goes a little too far in claiming that starch is almost exclusively digested by the pancreas. Bernard's experiments, however, were made chiefly on dogs, and these animals do not naturally take starch as food. In man, some of the starchy principles of the food are acted upon by the saliva, but, undoubtedly, most of the starch taken as food is digested in the small intestine. Although the intestinal juice is capable of effecting the transformation of starch into sugar, the experimental evidence is conclusive that in this it is subordinate to the pancreatic juice, which latter effects this transformation, at the temperature of the body, with extraordinary activity. There is no positive evidence that the bile has any thing to do with this action.

To sum up the whole process of the digestion of starch, it may be stated, in general terms, that this principle, when hydrated, which is the usual condition in which it is taken into the stomach of the human subject, is slightly acted upon by the saliva, both in the mouth and after it has passed into the stomach; when it is taken raw, it is hydrated in the stomach and usually undergoes no transformation into sugar until it has passed into the small intestine; and, when it passes out at the pylorus, mainly by the action of the pancreatic juice but with the assistance of the intestinal juice, it is transformed into glucose and in this form is absorbed.

We have already followed out the digestion of sugar as far as the small intestine. Glucose undergoes no change in the stomach and is taken directly into the circulation. It is probable, also, that a small quantity of cane-sugar may in like manner be taken up by the blood-vessels of the intestinal mucous membrane. It has been shown that a small quantity of cane-sugar is transformed into glucose in the stomach, but, as we noted in treating of stomach-digestion, the quantity is inconsiderable, and the transformation depends simply upon the presence of a free acid in the gastric juice.

As most of the saccharine principles of food exist in the form of cane-sugar, it is the action of the digestive fluids upon this variety of sugar which possesses the greatest physiological interest. As cane-sugar passes from the stomach into the duodenum it is almost instantly transformed into glucose. This fact has lately received additional confirmation in the case of intestinal fistula observed by Busch. In this case, when cane-sugar was introduced in quantity into the stomach, fasting, the fluid which escaped from the upper end of the intestine contained a small quantity of glucose but never any cane-sugar.

It now becomes a question whether the transformation of cane-sugar into glucose be effected by the bile, the intestinal juice, or the pancreatic juice. The pancreatic juice and the intestinal juice are the two fluids which might be supposed to have this effect; for it has been repeatedly demonstrated that the bile has of itself no direct action upon any of the alimentary principles. This point is settled by the experiments of Busch upon the lower end of the intestine, in his case of fistula. Matters introduced into this lower opening came in contact with the intestinal juice only. He found that cane-sugar, exposed thus to the action of the intestinal juice, was not converted into glucose, but a large portion of it was found in the fæces. His observations also indicate that cane-sugar is not readily absorbed by the intestinal mucous membrane until it has been transformed into glucose.

Out of the body, the pancreatic juice is capable, if kept but for a short time in contact with any of the saccharine principles, of transforming them into lactic acid. The contents of the small intestine are sometimes alkaline or neutral and are sometimes acid. When a very large quantity of sugar has been taken, a part of it may be converted in the intestine into lactic acid, and this may happen with the sugar which results from the digestion of starch; but, under ordinary conditions, starch and cane-sugar are readily changed into glucose and are absorbed without undergoing farther transformation. All the varieties of sugar, after they have been absorbed by the portal vein and carried to the liver, are here transformed into glucose, the only form, apparently, under which they can be used in nutrition.

Action of the Pancreatic Juice upon Nitrogenized Principles.—We have frequently had occasion to insist upon the great relative importance of intestinal digestion, and it has been apparent that, in the stomach, the process of disintegration of food is not final, even as regards many of the nitrogenized principles, but is rather preparatory to the complete liquefaction of these principles, which takes place in the small intestine. The experiments, already referred to, of Bernard, in which the pancreas has been partially destroyed in dogs, show rapid emaciation, with great voracity, and the passage, not only of unchanged fats and starch, but of undigested nitrogenized matter in the dejections.

In some instances, pieces of tripe which had been fed to the animal were recognizable in the fæces "by their aspect, because of their slight alteration." The voracious appetite, progressive emaciation, and the passage of all classes of alimentary substances in the fæces, after this operation, demonstrate conclusively the great importance of the pancreatic juice in digestion. But, when we inquire into the precise mode of action of this fluid upon the albuminoids, the question becomes one of great difficulty. If the bile be shut off from the intestine and discharged externally by a fistulous opening, the same voracity and emaciation are observed; and yet there is no single alimentary substance upon which the bile, of itself, can be shown to exert a decided digestive action. Farthermore, the pancreatic juice is evidently calculated to act upon alimentary principles after they have been subjected to the action of the stomach, a preparation which is absolutely essential to proper intestinal digestion; and, once passed into the intestine, the food comes in contact with a mixture of pancreatic juice, intestinal juice, and bile. We have to study, therefore, the special action of the pancreatic secretion upon the albuminoids, as far as it can be isolated, and its action in conjunction with the other intestinal fluids and in the presence of other alimentary principles in process of digestion. The first definite observations upon these points were made by Bernard. He found that the albuminoid substances generally, exposed to the action of the pancreatic juice out of the body, became rapidly softened and dissolved in some of their parts, but soon passed into a condition of putrefaction. An analogous change, it will be remembered, also takes place in starchy and fatty matters when exposed to the action of the pancreatic juice out of the body, and they pass through the various stages of transformation respectively into lactic acid and the fatty acids. This putrefactive action does not take place in albuminoids which have been precipitated after having been cooked, or in raw gluten or caseine. The presence of fat also interferes with putrefaction; so that Bernard concludes that the fats have an important influence in the intestinal digestion of nitrogenized principles.

Taking into consideration what has been positively ascertained concerning the action of the pancreatic juice upon the albuminoids, there can be no doubt with regard to the importance of its function in the digestion of these principles after they have been exposed to the action of the gastric juice. Experiments upon the digestion of these substances after they have passed out of the stomach show that they undergo important and essential changes as they pass down the intestinal canal. While the bile and the intestinal juice are by no means inert, they seem to be only auxiliary in their action to the pancreatic juice. When meat is taken into the stomach or is exposed even for a long period to the action of the gastric juice, there is always more or less insoluble residue, which can be shown by microscopical examination to consist of the muscular substance.

The preparation which the albuminoids undergo in the stomach is undoubtedly necessary to the easy digestion, in the small intestine, of that portion which is not dissolved by the gastric juice. This fact has been conclusively demonstrated by experiments on intestinal digestion in the inferior animals and by the observations of Busch in the case of intestinal fistula in the human subject.

Action of the Bile in Digestion.

A great deal of diversity of opinion has existed among physiologists concerning the functions of the bile. It is now pretty generally acknowledged that this fluid has, of itself, no marked influence upon any of the different classes of alimentary principles, such as we have observed in the other secretions discharged into the alimentary canal. This being the case, it is important to decide whether the bile be essential in assisting or modifying the action of other secretions or whether it be entirely inert in the digestive process. From the fact that it is poured into the upper part of the small intestine, it would seem that it must have some office, either in modifying the digestion and absorption of food or in the passage of alimentary substances or their residue down the intestinal tract. It is difficult to suppose that a fluid which is brought in contact with the alimentary mass in that portion of the intestine where the most important digestive processes commence should be simply excrementitious; yet this is the view entertained by some experimentalists. In this position of the subject, naturally the first question to decide relates to the excrementitious or recrementitious character of the bile; or whether, in other words, the bile be separated from the blood simply to be discharged from the body or have some important function to perform as a secretion. An apparently simple method of settling this question has been employed by many experimenters, but with results which are not satisfactory, unless they can be in some way harmonized. Schwann, Nasse, Bidder and Schmidt, and Bernard, whose observations will be more fully considered hereafter, have performed experiments upon animals in which the bile was entirely shut off from the intestine and discharged from the body by a fistula. If the bile be simply excrementitious, it should follow that animals operated upon in this way would not suffer from the discharge of the bile by a fistula and its diversion from the intestine; but, in all of them, death occurred with symptoms pointing to defective nutrition consequent upon grave disorder of digestion. The same result followed our own experiments on this subject. On the other hand, Blondlot attempts to show that the bile is simply an excretion, and that animals thrive and will live for an indefinite period, when the bile is diverted from its natural course and is discharged from the body.

In the experiments of those who simply closed the ductus communis choledochus, the effects of shutting off the bile from the intestine were modified by the consequent undue accumulation of this fluid in the biliary passages. The only way to obviate this difficulty was to discharge the bile by a fistula, as was first done by Schwann. The first experiments reported by Schwann were made upon sixteen dogs and one rabbit. Of these, only six can be regarded as successful; and, in the others, the animals either died of peritonitis resulting from the operation, or recovered, the fistulous opening into the gall-bladder becoming closed and the communication between the liver and the intestine re-establishing itself. These six animals died, apparently of inanition, respectively, after seven, thirteen, seventeen, twenty-five, sixty-four, and eighty days. In all, except the two animals that lived for sixty-four and eighty days respectively, there was gradual diminution in weight from the date of the operation, notwithstanding that a large quantity of food was taken. In the two exceptions, there was first diminution in weight, then the flesh was partially regained, but it subsequently diminished until death occurred. In these six animals, there was every reason to believe that death occurred from the abolition of the digestive function of the bile, and the disturbances in nutrition were very much like those produced by Bernard by destruction of the pancreas. These experiments were confirmed in their essential particulars by Bidder and Schmidt, Nasse, and Bernard. These facts seem to show that the bile is not simply an excrementitious fluid, and that its function, after it is discharged into the intestine, is not only important but absolutely essential to life. The only experiment which is opposed to this view is one reported by Blondlot.

The experiment by Blondlot was made upon a dog. The fistula was established in the fundus of the gall-bladder, the ductus communis having been tied and a portion exsected. Fifteen days after the operation, the animal had become extremely thin, but ate well, and, according to the report of the experimenter, was in perfect health. During all this time, however, he habitually licked the bile, but he was finally prevented from doing this by a muzzle. From the moment when the dog ceased to swallow the bile, the nutrition began to improve, and in three months he had recovered the natural amount of flesh. A farther account of this experiment is given by Blondlot in another memoir. The animal, while in perfect health aside from the existence of the fistula, was claimed by the owner, from whom it had been stolen before it passed into the hands of the experimenter. With the fistula still open, the dog was used by its owner for hunting and lived for five years. At the end of this time it was returned to M. Blondlot, but died while in his possession, two months after.

The important question then to determine was that the bile had been completely shut off from the intestinal canal. An examination of the parts was consequently made in the presence of a number of physicians and students. On the most minute dissection, it was impossible to find any communication between the bile-duct and the duodenum; and the conclusion arrived at was that the animal had lived for five years without a drop of bile passing into the intestine, and, consequently, that this fluid was useless in digestion.

The facts obtained by all other observers are in direct opposition to the above experiment. After a number of trials, we succeeded in establishing a biliary fistula in a dog, the operation being followed by no inflammation of the peritoneum, and, notwithstanding that the animal was voracious and consumed daily large quantities of food, it died in thirty-eight days, of inanition. If our own observation and those of other experimenters be correct, it is impossible that an animal should live in perfect health for years with all the bile discharged by a fistula.

There is reason to believe that the experiment of Blondlot was inaccurate, and that a communication existed between the bile-duct and the duodenum, which was not discovered at the dissection after death. The following observation strengthens us in this opinion:

We made an attempt on one occasion to ascertain the total amount of bile secreted in twenty-four hours; and, with this view, the ductus communis choledochus was exposed in a dog, the bile contained in the gall-bladder was pressed out, a canula, with an elastic bag attached, was fixed in the duct, and the external wound was closed, leaving the end of the canula, with the bag attached, protruding from the abdomen. The bag ruptured twenty-three hours after, and the experiment was consequently unsuccessful in the end for which it was undertaken. The tube dropped out at the end of forty-eight hours, and the external wound quickly healed. Thirty days after the operation the animal was killed. He had then entirely recovered, and no bile had been discharged externally for a long time. The alvine dejections were perfectly normal, and there could be no doubt that the bile was regularly discharged into the duodenum. On dissection after death, the liver was found normal, and the papilla which marks the opening of the bile-duct into the duodenum was natural in appearance. It was with the greatest difficulty, however, that the communication between the bile-duct and the duodenum could be found; yet, after patient searching for more than an hour, a small, tortuous tract was discovered. Had it not been certain that bile had been constantly discharged into the intestine, it might have been assumed, even after careful examination, that no such communication existed. This examination convinced us that it was possible that the communication between the duct and the intestine had been reëstablished in Blondlot's case, and that it had escaped observation in the dissection after death.

The isolated experiment of Blondlot does not therefore invalidate the results obtained by Schwann and confirmed by so many eminent physiologists. The bile is not simply an excretion but has an important and essential office to perform in the process of intestinal digestion. We have, however, conclusively shown that, in addition to its recrementitious function, it separates from the blood an important excrementitious principle, cholesterine, which, under a modified form, is discharged in the fæces. This function of the liver will be fully considered under the head of excretion. It is sufficient for our present purposes to show that the bile, unlike any other fluid in the organism, has two distinct functions, dependent upon two distinct classes of constituents. The peculiar principles known as the biliary salts, which are produced in the liver, give to it its digestive properties; and the cholesterine, which is simply separated from the blood by the liver, gives it its excrementitious character.

As we are much better acquainted with the excrementitious than with the digestive function of the bile, we shall consider, in this connection, only a few of the points concerning the chemistry of this fluid, deferring a full account of its composition until we come to treat of it as an excretion.

The bile varies in color and consistence in different animals. It usually has a greenish, yellowish, or brownish hue. In the human subject, it has a dark, golden-brown color and is somewhat viscid in consistence, chiefly from admixture with the mucus of the gall-bladder. The specific gravity of human bile has been found to be about 1018. Its reaction is faintly alkaline.

Physiological chemists have long since recognized in the bile peculiar principles, which are found in no other part of the organism; but the exact nature of these constituents was first described by Strecker, in 1848, who obtained from the bile of the ox two principles, cholic and choleic acid, which he found to exist in this fluid in combination with soda. The cholic acid of Strecker, which may be decomposed into a new acid and a principle called glycine, and the choleic acid, from which may be formed a new acid and taurine, are called by Lehmann, respectively, glycocholic and taurocholic acid. In the bile of the ox, these are found combined with soda, and the peculiar proximate principles of this fluid are now recognized as the glycocholate of soda, a crystalline substance, and the taurocholate of soda, which is of a resinous consistence and is stated to be uncrystallizable. In the human bile, Dalton has found a resinous substance, which, from its behavior with various reagents, is undoubtedly analogous to the taurocholate of soda of ox-bile, but which he could not obtain in a crystalline form.

FIG. 77.—*Crystals of glycocholate of soda.* (Robin.)

In addition to the biliary salts, the bile contains the ordinary inorganic salts, found in nearly all the animal fluids, a small quantity of fat, the oleates, margarates, and stearates of soda and potassa, mucus from the gall-bladder, and cholesterine; the last being an excrementitious product. The action of the bile in digestion, whatever its nature may be, undoubtedly depends chiefly upon the biliary salts, and perhaps to some extent upon its saponaceous constituents.

Experiments with regard to the action of the bile upon different alimentary substances out of the body have not led to any definite results. It is only in connection with the other digestive fluids that the bile seems to be efficient; and the only observations which have thrown any light upon the subject are those made upon digestion in the living organism. Simple ligation of the bile-duct has taught us very little regarding the effects of shutting off the bile from the intestine; for the immediate effects of the operation generally interfered with the process of digestion, and subsequently the experiment was necessarily disturbed by the effects of the retention of bile in the excretory passages. As would naturally be expected, these observations have been quite contradictory. The most satisfactory experiments upon the digestive function of the bile have followed the establishment of a fistulous opening into the gall-bladder, the flow of bile at the same time being completely shut off from the intestine. In all experiments of this kind in which fatal inflammation did not follow the operation, death has taken place from inanition, notwithstanding an increase in the quantity of food taken. This result is not due simply to the loss of the solid matter discharged in the bile, which is small in proportion to the total daily loss of weight; but it undoubtedly proceeds from disordered nutrition, which has its starting-point in disordered digestion.

Observations on a Dog with a Biliary Fistula.—We have now to study the modifications in digestion and nutrition which are the result of simply diverting the bile from the intestine. With that view, we followed carefully these changes in an animal with a biliary fistula that was under our own observation. This experiment confirmed, in all important particulars, those of Schwann and of Bidder and Schmidt. It is given here somewhat in detail, for, inasmuch as no inflammation followed the operation and nothing occurred to complicate the effects of the diversion of the bile from the intestine, we regarded the experiment as remarkably successful.

November 15, 1861, a biliary fistula was established in a young cur-dog weighing twelve pounds. The abdominal organs were very little exposed, and the experiment, from the first, promised to be very satisfactory. The bile-duct was first ligated next the intestine and at its junction with the cystic duct, and the intermediate portion was exsected. The incision in the abdomen was in the median line just below the ensiform cartilage, and was about three inches long. The fundus of the gall-bladder was then drawn to the upper portion of the wound, and the bile was evacuated by a small opening, the edges of which were attached to the abdominal parietes. The wound in the abdomen was then closed, except the opening into the gall-bladder, into which a few shreds of lamp-wicking were introduced.

The animal appeared to do perfectly well after the operation and ate the usual quantity the next day. He was kept in a warm room, although the weather was mild; and a careful record was made of his condition every day. The fistula occasionally showed a tendency to close, but it was kept open by the occasional introduction of a glass rod. From time to time, while the animal was under observation, he licked the bile as it flowed from the fistula. This was afterward prevented by a long wire-muzzle, the sides of which were covered with oil-silk.

The abdomen was somewhat tumid, with some rumbling in the bowels, for five days after the operation. The first alvine discharge took place on the evening of the second day. The fæces seemed in all regards normal. After that time, they became very infrequent, although the animal ate well every day. The fæces that were passed after the third day were of a grayish color and moderately soft. They had an exceedingly offensive and penetrating odor. At about the fifteenth day, the fæces became more frequent, and, from that time, were passed three or four times a day. Generally, they were clay-colored; but on one or two occasions they were quite dark. They always had a peculiarly offensive odor.

The weight of the animal remained stationary for about four days. On the sixth day (November 20th), the weight began to diminish. He weighed on that day, before feeding, eleven and one-quarter pounds. November 22d, he weighed but little over eleven pounds. November 24th, he weighed ten pounds. He maintained this weight until December 1st, when the weight again began to diminish. On December 6th, the weight was nine pounds. On December 7th, the weight was reduced to eight and a half pounds, and the strength began to fail manifestly. December 10th and 11th, he gained a little, on those days weighing nine pounds; but, after that, he progressively diminished in strength and in weight until death occurred, thirty-eight days after the operation. The weight was then seven and a half pounds, showing a total loss of four and a half pounds, or 37½ per cent.

During the first nine days of the observation, the animal ate well but not ravenously, taking about three-quarters of a pound of beef-heart daily. On the tenth day, the appetite increased. He ate on that day, at one time a pound, and at another, half a pound of meat. He ate on an average about a pound and a half of beef-heart daily, until the day before his death. During the last five or six days, he seemed very ravenous and was not allowed to eat all that he would at one time. At this time he was ordinarily fed twice a day. He would not eat fat, even when very hungry. During the last day, when too

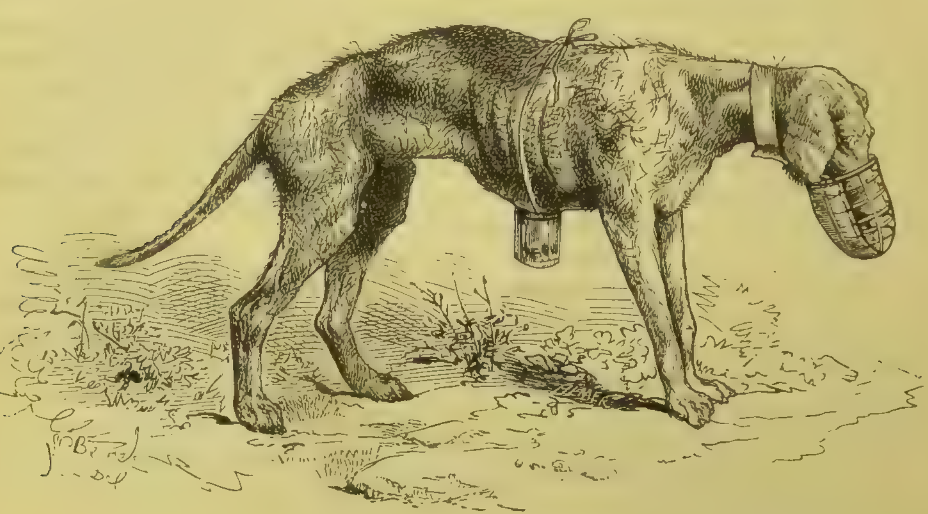


Fig. 78.—*Dog with a biliary fistula.*

From a rough sketch made the fourteenth day after the operation. A small glass vessel is tied around the body to collect the bile, and a wire muzzle, the lower part of which is covered with oil-silk, is placed over the mouth to prevent the animal from licking the bile. The dog is considerably emaciated.

weak to stand, he attempted to eat while lying down. During the last twelve days of the observation, he attempted constantly to eat the fæces. During the last days of the experiment, when the dog had become much reduced in weight, he became very cross and snapped at every animal that came near him. There was never any icterus, fetor of the breath, or falling off of the hair.

A careful examination of the animal was made after death. The gall-bladder was somewhat contracted but not obliterated, and the fistula would admit a large-sized male catheter. Both ends of the divided bile-duct were found impervious, and there was no passage of bile into the intestine. The abdominal organs were normal, with the exception of evidences of slight peritoneal inflammation around the wound and over the convex surface of the liver. There was no fat in the omentum or anywhere in the body, except a very small quantity at the bottom of the orbit.

The above observation is a type of the instances—which are not very numerous—in which the bile has been completely shut off from the intestine and discharged externally by a fistula into the gall-bladder. As far as could be ascertained, this animal, from the first, presented no disturbances which were not due solely to the absence of the bile from the intestine and its discharge externally. Although the phenomena here presented do not teach us much that is definite concerning the digestive action of the bile, taken in connection with what has been ascertained concerning the general properties of this secretion, they throw some light upon its functions.

One of the functions which has been ascribed to the bile is that of regulating the peristaltic movements of the small intestine and of preventing putrefactive changes in the intestinal contents and the abnormal development of gas. Experiments on this point are somewhat conflicting. Our own observations would lead us to doubt the constant influence of the bile upon the peristaltic movements. During the first few days of our experiment, the dejections were very rare; but they afterward became regular, and, at one time, even, there was a tendency to diarrhœa. There can be no doubt, however, that the bile retards the putrefaction of the contents of the intestinal canal, particularly when animal food has been taken. The fæces in the dog were always extremely offensive. Bidder and Schmidt found this to be the case in dogs fed entirely on meat; but the fæces were nearly odorless when the animals were fed on bread alone. In the case of intestinal fistula in the human subject, the evacuations which took place after the introduction of alimentary substances into the lower portion of the intestine had an unnaturally offensive and putrid odor. In this case, as it was impossible for matters to pass from the portions of the intestine above the fistula to those below, the food introduced into the lower opening was completely removed from the action of the bile.

As far as the digestion of the different alimentary principles is concerned, it has been shown that the bile, of itself, has no particular action upon any of them. In the fæces of animals with biliary fistula, the only peculiarity which has been observed, aside from the putrefactive odor and the absence of the coloring matter of the bile, has been the presence of an abnormal proportion of fat. We have observed this in the fæces of a patient suffering under jaundice apparently due to temporary obstruction of the bile-duct. This fact was noted in the dogs experimented upon by Bidder and Schmidt.

The various experiments which have been performed upon animals render it almost certain that the bile has an important influence, either upon the digestion or upon the absorption of fats. Bidder and Schmidt noted in animals with biliary fistula that the chyle contained very much less fat than in health. In an animal with a fistula and the bile-duct obliterated, the proportion of fat was 1·90 parts to 1,000 parts of chyle; while, in an animal with the biliary passages intact, the proportion was 32·79 parts per 1,000. In animals operated upon in this way, there is frequently a great distaste for fatty articles of food. In our own observation, the dog refused fat meat, even when very hungry and when lean meat was taken with great avidity.

Experiments concerning the influence of the bile upon the absorption of fats have resulted in hardly any thing definite. We know only the fact that, when the bile is diverted from the intestine, the proportion of fat in the chyle is greatly reduced, and a large proportion of the fat taken with the food passes through the intestine and is found in the fæces.

The action of the bile in exciting muscular contraction, particularly in the smooth muscular fibres, is pretty well established. It has been shown by Schiff that this fluid acts upon the muscular fibres situated in the substance of the intestinal villi, causing them to contract, and, according to his view, assisting in the absorption of chyle by emptying the lacteals of the villi. The whole subject, however, of the absorption of fats is exceedingly difficult of investigation; and our knowledge of it has not been sensibly advanced by the experiments upon the influence exerted by the bile. Notwithstanding the obscurity in which this subject is involved, it is certain that the progressive emaciation, loss of strength, and final death of animals deprived of the action of the bile in the intestime, are due to defective digestion and assimilation. In spite of the great quantities of food taken by these animals, the phenomena which precede the fatal result are simply those of starvation. It may be that the biliary salts are absorbed by the blood and are necessary to proper assimilation; but there is no experimental basis for this supposition, and it is impossible to discover these salts in the blood of the portal system by the ordinary tests. It is more probable that the biliary salts influence in some way the digestive process and are modified and absorbed with the food.

The observations of Bidder and Schmidt show conclusively that the characteristic constituents of the bile are absorbed in their passage down the alimentary canal. Having arrived at a pretty close estimate of the quantity of bile daily produced in dogs, they collected and analyzed all the fæcal matter passed by a dog in five days. Of the dry residue of the fæces, the proportion which could by any possibility represent the biliary matters did not amount to one-fourth of the dry residue of the bile which must have been secreted during that time. They also estimated the total quantity of sulphur contained in the fæces and found that the entire quantity was hardly one-eighth of that which was discharged into the intestine in the bile; and, inasmuch as nearly one-half of that found in the fæces came from hairs which had been swallowed by the animal, the experiment showed that nearly all the sulphur contained in the non-crystallizable element of the bile (the taurocholate of soda) had been taken up again by the blood. These observations show conclusively that the greater part of the bile, with the biliary salts, is absorbed by the intestinal mucous membrane. Prof. Dalton has attempted to follow these principles into the blood of the portal system, but has never been able to detect the biliary salts, by the most careful analysis. Like the peculiar principles of other secretions which are reabsorbed in the alimentary canal, these substances become changed and are not to be recognized by the ordinary tests, after they are taken into the blood.

Although it is the digestion and absorption of fatty substances which seem to be most seriously interfered with in cases of biliary fistula in the inferior animals, the rapid loss of weight and strength indicates great disturbance in the digestion and absorption of other articles of food. A fact which indicates a connection between the bile and the process of digestion is that the flow of this secretion, although constant, is greatly increased when food passes into the intestinal canal. This has been noted by all who have experimented on the subject. The following observations on the dog, showing the variations in the flow of bile from the fistula, were made twelve days after the fistula had been established, when the weight of the animal had been reduced from twelve to ten pounds.

Table of Variations in the Flow of Bile with Digestion.

(At each observation, the bile was drawn for precisely thirty minutes.)

Time after Feeding.	Fresh Bile.	Dried Bile.	Percentage of Dry Residue.
	Grains.	Grains.	
Immediately	8·103	0·370	4·566
One hour	20·527	0·586	2·854
Two hours	35·760	1·080	3·023
Four hours	38·939	1·404	3·605
Six hours	22·209	0·987	4·450
Eight hours	36·577	1·327	3·628
Ten hours	24·447	0·833	3·407
Twelve hours	5·710	0·247	4·325
Fourteen hours	5·000	0·170	3·400
Sixteen hours	8·643	0·309	3·575
Eighteen hours	9·970	0·277	2·778
Twenty hours	4·769	0·170	3·565
Twenty-two hours	7·578	0·293	3·866

Disregarding slight variations in this table, which might be accidental, it may be stated, in general terms, that the bile commences to increase in quantity immediately after eating; that its flow is at its maximum from the second to the eighth hour, during which time the quantity does not vary to any great extent; after the eighth hour it begins to diminish, and, from the twelfth hour to the time of feeding, it is at is minimum.

Although it has been pretty satisfactorily demonstrated that the presence of the bile in the small intestine is necessary to proper digestion and even essential to life, and although the variations in the flow of bile with digestion are now well established, it must be confessed that we have scarcely any definite information concerning the mode of action of the bile in intestinal digestion and absorption. Nearly all that we can say on this point is that its action seems to be auxiliary to that of the other digestive fluids.

Movements of the Small Intestine.

By the contractions of the muscular coat of the small intestine, the alimentary mass is made to pass along the canal, sometimes in one direction and sometimes in another; the general tendency, however, being toward the cæcum. The partially-digested matters which pass out at the pylorus are prevented from returning to the stomach by the peculiar arrangement of the fibres which constitute the pyloric muscle. The passage from the stomach to the intestine, as we have seen, becomes constricted gradually, so that food of the proper consistence finds its way easily into the duodenum; but, viewed from the duodenal side, the constriction is abrupt, so that regurgitation is generally difficult.

Once in the intestine, the food is propelled along the canal by peculiar movements, which have been called peristaltic, when its direction is toward the large intestine, and antiperistaltic, when the direction is reversed. These movements are of the character peculiar to the unstriped muscular fibres; viz., slow, gradual, the contraction enduring for a certain time and being followed by a correspondingly slow and gradual relaxation. Both the circular and the longitudinal muscular layers participate in these movements. If we carefully watch this action in the intestines of an animal after the abdomen has been opened, we can sometimes see a gradual constriction produced by the action of the circular fibres at a certain point, which is slowly propagated along the tube, while, at the same time, the longitudinal fibres are alternately contracted and relaxed in the same gradual manner, shortening and elongating the tube and facilitating the onward passage of its contents. It can readily be appreciated how movements of this kind are capable of propelling the alimentary mass slowly but certainly along the intestinal tract, even when the direction is in opposition to the force of gravity; and we can see how admirably these movements are calculated to thoroughly incorporate the food with the digestive fluids and to expose those parts which have been completely liquefied to the absorbent action of the mucous membrane.

Although the mechanism of the propulsive movements of the intestine may be studied in living animals after opening the abdomen, or, better still, in animals just killed, the movements thus observed do not entirely correspond with those which take place under natural conditions. In vivisections, no movements are observed at first; but, soon after exposure of the parts, nearly the whole intestine moves like a mass of worms. In the normal process of digestion, the movements are never so general or so active; they take place more regularly and consecutively in those portions in which the contents are most abundant, and the movements are generally intermittent, being interrupted by long intervals of repose. In Prof. Busch's case of intestinal fistula, there existed a large ventral hernia, the coverings of which were so thin that the peristaltic movements could be readily observed. In this case, the general character of the movements corresponded with what has been observed in the inferior animals. It was noted that the movements were not continuous, and that there were often intervals of rest for more than a quarter of an hour.

It was also observed that the movements, as indicated by flow of chymous matter from the upper end of the intestine, were intermitted with considerable regularity during part of the night. Antiperistaltic movements, producing discharge of matters which had been introduced into the lower end of the intestine, were frequently observed.

As far as has been ascertained by observations upon the human subject and warm-blooded animals, the regular intestinal movements are excited by the passage of alimentary matter from the stomach through the tube during the natural process of digestion. By a very slow and gradual action of the muscular coat of the intestine, its contents are passed along, occasionally the action being reversed for a time, until the indigestible residue, mixed with a certain quantity of intestinal secretion, more or less modified, is discharged gradually into the caput coli. These movements are apparently not continuous, and they depend somewhat upon the quantity of matter contained in different parts of the intestinal tract. If we are to judge from the movements in the inferior animals after the abdomen has been opened, the intestines are constantly changing their position, principally by the action of their longitudinal muscular fibres, so that the force of gravity does not oppose the onward passage of their contents as much as if the relative position of the parts were constant. There are no definite observations concerning the relative activity of the peristaltic movements in different portions of the intestine; but, from the fact that the jejunum is constantly found empty, while the ileum contains a considerable quantity of pultaceous matter, it would seem that the movements must be more vigorous and efficient in the upper portions of the canal.

The gases which are constantly found in the intestine have an important mechanical function. They are useful, in the first place, in keeping the canal constantly distended to the proper extent, thus avoiding the liability to disturbances in the circulation and facilitating the passage of the alimentary mass in obedience to the peristaltic contractions. They also support the walls of the intestine and protect these parts against concussions in walking, leaping, etc. The gases are useful, likewise, in offering an elastic but resisting mass upon which the compressing action of the abdominal muscles may be exerted in the acts of straining and expiration. If we could suppose the intestinal tube to be entirely free from gaseous contents, it is evident that the functions above mentioned would be performed imperfectly and with difficulty.

There can be hardly any question that the normal movements of the intestine are due principally to the impression made upon the mucous membrane by the alimentary matters, to which is added, perhaps, the stimulating action of the bile. It is difficult to determine with accuracy what part the bile plays in the production of these movements, from the fact that the normal action of the intestine is not easily observed. In the case of intestinal fistula so often referred to, when food was introduced into the lower end of the canal, there was at first an abundant evacuation every twenty-four hours; but subsequently it became necessary to use enemeta. As there was no communication between the lower and the upper end of the intestine, this fact is an evidence that the peristaltic movements can take place without the action of the bile. Experiments upon the inferior animals concerning the influence of the bile upon the peristaltic movements are somewhat contradictory. When the abdomen is opened during life, vigorous movements may sometimes be excited by pressing bile into the intestine from the gall-bladder; and the same result is occasionally observed when the bile is applied to the peritoneal surface in an animal recently killed. But the various experiments in which the bile has been diverted from the intestine and discharged by a fistula, taking the frequency of the alvine dejections as a test, show that regular peristaltic movements may take place without the intervention of the bile.

The vigorous peristaltic movements which occur soon after death have been explained in various ways. It has been shown that these movements are not due to a lowering of the temperature or to exposure of the intestines to the air. The latter fact may be easily verified by killing a rabbit, when vigorous movements may be seen through the thin abdominal walls, even while the cavity is unopened. According to Schiff, the only cause of these exaggerated movements is diminution or arrest of the circulation. This physiologist, by compressing the abdominal aorta in a living animal, was able to excite peristaltic movements in the intestine as vigorous as those which take place after death; and, on ceasing the compression, the movements were arrested.

The nerves distributed to the small intestine are derived from the sympathetic, and from branches of the pneumogastric, which latter come from the nerve of the right side and are distributed to the whole of the tract, from the pylorus to the ileo-cæcal valve. The intestine receives no filaments from the left pneumogastric. The experiments of Brachet, by which he attempted to prove that the movements of the intestines were under the control of the pneumogastric and nerves emanating from the spinal cord, have not been verified by other observers. Recent experiments render it probable that an influence, derived from the cerebro-spinal system, is essential to the functions of the sympathetic ganglia, which may account for some of the results obtained by Brachet after dividing the spinal cord. The experiments of Müller, however, render it certain that the peristaltic movements are to some extent under the influence of the sympathetic system. In these experiments, movements of the intestine were produced by galvanization of filaments of the sympathetic distributed to its muscular coat, after the ordinary post-mortem movements had ceased. The same results followed the application of caustic potash to the semilunar ganglia, the movements reappearing when the potash was applied, "with extraordinary vivacity" in the rabbit, after the abdomen had been opened and the movements had entirely ceased. These experiments have been confirmed by Longet, who found, however, that the movements did not take place unless alimentary matters were contained in the intestine.

It must be acknowledged that very little is known concerning the reflex actions which take place through the sympathetic system; but there is certainly good ground for supposing that certain reflex functions are performed by this system of nerves, one of the most important of which is the production of peristaltic movements in obedience to the impression made by alimentary substances upon the mucous membrane. This impression is probably conveyed to the semilunar ganglia and reflected back through the motor nerves to the muscular coat of the intestine.

Physiological Anatomy of the Large Intestine.

The large intestine, so called because its diameter is greater than that of the rest of the intestinal tract, receives for the most part only the indigestible residue of the food, mingled with certain of the secretions which are discharged into the small intestine. In the human subject, the processes of digestion which take place in this part of the alimentary canal are unimportant; and it is probable that, under physiological conditions, hardly any thing but water is absorbed by its lining membrane. Matters are, however, stored up in the large intestine for a number of hours, and a certain amount of secretion takes place from its follicular glands.

The entire length of the large intestine is from four to six feet. Its diameter is greatest at its commencement, where it measures, when moderately distended, from two and a half to three and a half inches. According to the observations of Brinton, the average diameter of the tube beyond the cæcum is from one and two-thirds to two and two-thirds inches. Passing from the cæcum, the canal diminishes in caliber, gradually and very slightly, to where the sigmoid flexure opens into the rectum. This is the narrowest portion of the canal. Beyond this, the rectum gradually increases in diameter, forming a kind of pouch, which abruptly diminishes in size near the external opening, to form the anus.

The general direction of the large intestine is from the cæcum in the right iliac fossa to the left iliac fossa, thus encircling the convoluted mass formed by the small intestine, in the form of a horseshoe. From the cæcum to the rectum, the canal is known as the colon. The first division of the colon, called the ascending colon, passes almost directly upward to the under surface of the liver; the canal here turns at nearly a right angle, passes across the upper part of the abdomen, and is called the transverse colon; it then passes downward at nearly a right angle, forming the descending colon. The last division of the colon, called the sigmoid flexure, is situated in the left iliac fossa and is in the form of the italic letter *S*. This terminates in the rectum, which is not straight, as its name would imply, but presents at least three distinct curvatures, as follows: it passes first in an oblique direction from the left sacro-iliac symphysis to the median line opposite the third piece of the sacrum; it then passes downward, in the median line, following the concavity of the sacrum and coccyx; and the lower portion, which is about an inch in length, turns backward to terminate in the anus.

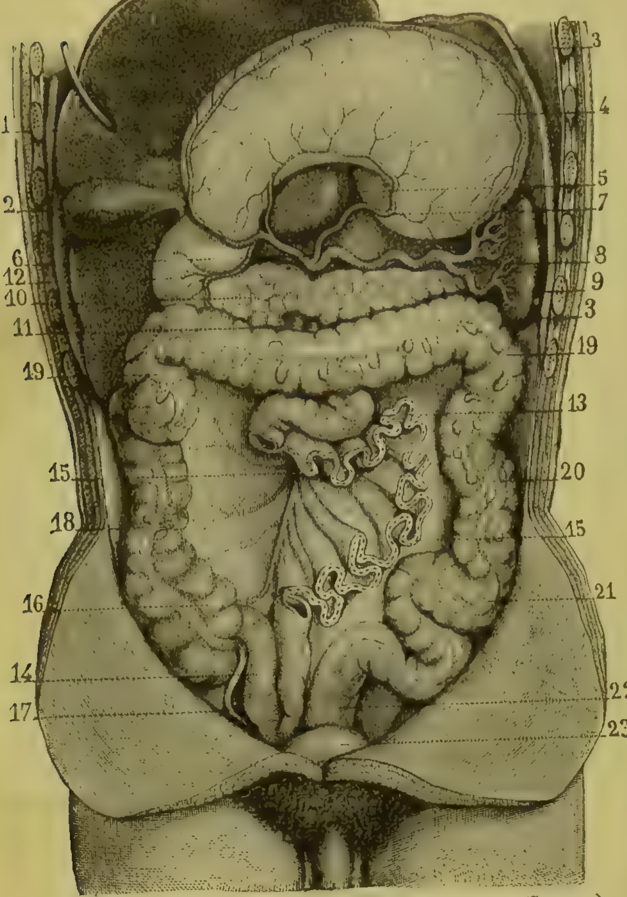


FIG. 79.—*Stomach, pancreas, large intestine*, etc. (Sappey.)
1, anterior surface of the liver; 2, gall-bladder; 3, 3, section of the diaphragm; 4, posterior surface of the liver; 5, lobus Spigelii of the liver; 6, cœliac axis; 7, coronary artery of the stomach; 8, splenic artery; 9, spleen; 10, pancreas; 11, superior mesenteric vessels; 12, duodenum; 13, upper extremity of the small intestine; 14, lower end of the ileum; 15, 15, mesentery; 16, *cæcum*; 17, *appendix vermiformis*; 18, *ascending colon*; 19, 19, *transverse colon*; 20, *descending colon*; 21, *sigmoid flexure of the colon*; 22, *rectum*; 23, urinary bladder.

The form of the large intestine is peculiar. The cæcum, or caput coli, presents a rounded, dilated cavity, continuous with the colon above and communicating by a transverse slit with the ileum. At its lower portion, is a small, cylindrical tube, from one to five inches in length, opening below and a little posterior to the opening of the ileum, called the vermiform appendix. This is covered with peritoneum and is possessed of a muscular and a mucous coat. It is sometimes entirely free and is sometimes provided with a short fold of mesentery for a part of its length. The coats of the appendix are very thick. The muscular coat consists of longitudinal fibres only. The mucous membrane is provided with tubules and closed follicles, the latter frequently being very numerous. This little tube, which is only about one-third of an inch in diameter, generally contains a quantity of clear, viscid mucus. The uses of the vermiform appendix are unknown.

Ileo-cæcal Valve.—The most interesting anatomical peculiarity of the cæcum is the opening by which it receives the contents of the small intestine. This opening is arranged in the form of a valve, known as the ileo-cæcal valve, situated at the inner and posterior portion of the cæcum. The small intestine, at its termination, presents a shallow concavity, which is provided with a horizontal, button-hole slit opening into the cæcum. The surface of the valve which looks toward the small intestine is covered with a mucous membrane provided with villi and in all respects resembling the general mucous lining of the small intestine. Viewed from the cæcum, a convexity is observed corresponding to the concavity upon the other side. The cæcal surface of the valve is covered with a mucous membrane identical with the general mucous lining of the large intestine. It is evident, from an examination of these parts, that pressure from the ileum would open the slit and allow the easy passage of the semifluid contents of the intestine; but pressure from the cæcal side approximates the lips of the valve, and the greater the pressure the more firmly is the opening closed. The valve itself is composed of folds formed of the white fibrous tissue of the intestine (the cellular tunic of some anatomists), and circular muscular fibres from both the small and the large intestine, the whole being covered with mucous membrane. The lips of the valve unite at either extremity of the slit and are prolonged on the inner surface of the cæcum, forming two raised bands or bridles; and these become gradually effaced and are thus continuous with the general lining of the canal. The posterior bridle is a little longer and more prominent than the anterior. These assist somewhat in enabling the valve to resist pressure from the cæcal side. The longitudinal layer of muscular fibres and the peritoneum pass directly over the attached edge of the valve and are not involved in its folds. These give strength to the part, and, if they be divided over the valve, gentle traction will suffice to draw out and obliterate the folds, leaving a simple and unprotected communication between the large and the small intestine.

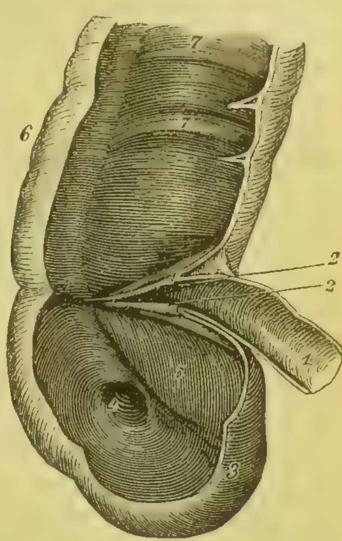


FIG. 80.—*Opening of the small intestine into the cæcum.* (Le Bon.)
1, small intestine; 2, ileo-cæcal valve; 3, cæcum; 4, opening of the appendix vermiformis; 5, mucous fold at the opening of the appendix; 6, large intestine; 7, 7, folds of the mucous membrane.

Peritoneal Coat.—Like most of the other abdominal viscera, the large intestine is covered by peritoneum. The cæcum is covered by this membrane only anteriorly and laterally. It is usually bound down closely to the subjacent parts, and its posterior surface is without a serous investment; although sometimes it is completely covered, and there may be even a short mesocæcum. The ascending colon is likewise covered with peritoneum only in front and is closely attached to the subjacent parts. The same arrangement is found in the descending colon. The transverse colon is almost completely invested with peritoneum; and the two folds forming the transverse mesocolon separate to pass over the tube above and below, uniting again in front to form the great omentum. The transverse colon is consequently quite movable. In the course of the colon and the upper part of the rectum, particularly on the transverse colon, are found a number of little sacculated pouches filled with fat, called the appendices epiploïcæ. The sigmoid flexure of the colon is invested with peritoneum, except at the attachment of the iliac mesocolon. This division of the intestine is capable of considerable motion. The upper portion of the rectum is almost completely covered by peritoneum and is but loosely held in place. The middle portion is closely bound down, and is covered with peritoneum only anteriorly and laterally. The lowest portion of the rectum has no peritoneal covering.

Muscular Coat.—The muscular fibres of the large intestine have an arrangement quite different from that which exists in the small intestine. The external, longitudinal layer, instead of extending over the whole tube, is arranged in three distinct bands, which commence in the cæcum at the vermiform appendix. Passing along the ascending colon, one of the bands is situated anteriorly, and the others, latero-posteriorly. In the transverse colon, the anterior band becomes inferior and the two latero-posterior bands become respectively postero-superior and postero-inferior. In the descending colon and the sigmoid flexure, the muscular bands resume the relative position which they had in the ascending colon. As these longitudinal fibres pass to the rectum, the anterior and the external bands unite to pass down on the anterior surface of the canal, while the posterior band passes down on its posterior surface. Thus the three bands are here formed into two. These two bands as they pass downward, though remaining distinct, become much wider; and longitudinal muscular fibres commencing at the rectum are situated between them, so that this part of the canal, especially in its lower portion, is covered with longitudinal fibres in a pretty uniform layer.

The arrangement of the muscular fibres of the rectum has been closely studied by Sappey. He has found that, as far as their terminations are concerned, the fibres may be divided into an external, a middle, and an internal layer. The posterior fibres of the external layer pass away from the lower portion of the rectum, are reflected backward along the concavity of the sacrum, and are attached to the promontory. These fibres, which are generally pale, Sappey proposes to designate as retractors of the anus. A few of the posterior fibres are attached to the aponeurosis and the parts between the coccyx and the promontory. In front, the external fibres are attached to the aponeurosis which covers the vesiculæ seminales, and laterally they are inserted into the deep pelvic fascia. The termination of the middle layer of the fibres is less clearly made out. Those situated at the sides of the rectum are inserted into "a very dense cellulo-fibrous band, which, by its opposite surface, gives insertion to a great number of fibres of the levator ani." The others are many of them continuous with the fibres of the levator ani as they pass along the floor of the pelvis. Some of the fibres of the deep layer are attached by little tendons, which pass between the external and the internal sphincter, to the deep portions of the skin encircling the anus. The importance of closely studying the attachments of these fibres will be appreciated when we come to treat of defæcation.

Over the cæcum and the colon, the anterior band of muscular fibres is from one-third to one-half an inch in width. The postero-external band is not more than half so wide, and the postero-internal band is even narrower. The muscular bands are much shorter than the canal itself, and their attachment to the walls gives the intestine a peculiar sacculated appearance. That this is produced by the arrangement of the muscular fibres, may be demonstrated by dividing them in various places or by removing them entirely, when the canal may be extended to double its original length. Between the bands there are no longitudinal muscular fibres; but circular or transverse muscular fibres exist throughout the whole length of the large intestine. In the cæcum and the colon, the circular fibres are so pale and the layers are so thin that their presence is demonstrated with great difficulty. In the rectum they are somewhat more numerous. About an inch above the anus, the circular fibres are collected into a pretty well-marked muscular ring, which has been called the internal sphincter.

Mucous Coat.—The mucous lining of the large intestine presents several important points of difference from that which is found in the small intestine. It is paler, somewhat thicker and firmer, and is more closely adherent to the subjacent parts. In no part of this membrane are there any folds, like those which form the valvulæ conniventes of the small intestine; and the surface is perfectly smooth and free from villosities.

Throughout the entire mucous membrane, from the ileo-cæcal valve to the anus, are innumerable orifices which lead to simple follicular glands. These structures resemble in all respects the follicles of the small intestine, except that they are a little longer, owing to the greater thickness of the membrane, are wider, and are rather more numerous. Among these small follicular openings are found, scattered irregularly throughout the membrane, larger openings which lead to utricular glands, resembling the closed follicles, in general structure, except that they have an orifice opening into the cavity of the intestine, which is sometimes so large as to be visible to the naked eye. The number of these glands is very variable, and they are irregularly disseminated throughout the intestine, in company with the closed follicles, except in the rectum, where they are absent. In the cæcum and colon, numerous isolated, closed follicles are generally found, which are identical in structure with the solitary glands of the small intestine. These are exceedingly variable, both in number and size.

The mucous membrane of the rectum, in the upper three-fourths of its extent, does not differ materially from that of the colon. In the lower fourth, the fibrous tissue by which the lining membrane is united to the subjacent muscular coat is loose, and the membrane, when the canal is empty, is thrown into a great number of irregular folds. At the site of the internal sphincter, five or six little semilunar valves have been observed, with their concavities directed toward the colon. These form an irregular, festooned line, which surrounds the canal; their folds, however, are small and have no tendency to obstruct the passage of fæcal matters. The simple follicles are particularly abundant in the rectum, and the membrane is constantly covered with a thin coating of mucus. Another peculiarity to be noted in the mucous membrane of the lower portion of the rectum, is its great vascularity, the veins, especially, being very numerous.

Finally, the rectum terminates in the anus, a button-hole orifice, situated a little in front of the coccyx, which is kept closed and somewhat retracted, except during the passage of the fæces, by the powerful external sphincter. This muscle is composed entirely of red, or striated fibres, which are arranged in the form of an ellipse, its long diameter being antero-posterior.

It is now almost universally admitted that the digestion of all classes of alimentary substances is completed either in the stomach or in the small intestine, and that the mucous membrane of the large intestine does not secrete a fluid endowed with any well-marked digestive properties. The simple follicles, the closed follicles, and the utricular glands, produce a glairy mucus, which, as far as we know, serves merely to lubricate the canal. This has never been obtained in sufficient quantity to admit of any accurate investigation into its properties.

In studying the changes which the alimentary mass undergoes in its passage through the small intestine, we have seen that, in this portion of the canal, the greatest part of all the nutritive material is not only liquefied but is absorbed. Sometimes fragments of muscular fibre, oil-globules, and other matters in a state of partial disintegration, are to be detected in the fæces by the microscope; but generally this is either the result of taking an excessive quantity of these substances or it depends upon some derangement of the digestive apparatus. When intestinal digestion takes place with regularity, the transformation of the alimentary mass into fæcal matter is slow and gradual. As the contents of the stomach are passed little by little into the duodenum, the chymous mass becomes of a bright-yellow color, and its fluidity is increased, from the admixture of bile and pancreatic fluid. In passing along the canal, the consistence of the mass gradually diminishes, from the absorption of its liquid portions, and the color becomes darker; and, by the time that the contents of the ileum are ready to pass into the cæcum, the greatest part of those substances which we have recognized as alimentary principles have become changed and absorbed. The various forms of starchy and saccharine principles, unless they have been taken in excessive quantity, soon disappear from the intestine; and the glucose, which is the result of their digestion, may be recognized in the blood of the portal system. As a rule, fatty matters are not found in the lower part of the ileum, having passed into the lacteals in the form of an emulsion. Neither fibrin, albumen, nor caseine, can be detected in the ileum; and, as we have seen, the muscular substance, as recognized by its microscopical characters, becomes gradually disintegrated and is lost—except a few isolated fragments deeply colored with bile—some time before the indigestible residue passes into the large intestine.

In the human subject, those portions of the food which resist the successive and combined action of the different digestive secretions are derived chiefly from the vegetable kingdom. Hard, vegetable seeds, the cortex of the cereals, spiral vessels, and, in fine, all parts which are composed largely of cellulose, pass through the intestinal canal without much change. These substances form, in the fæces, the greatest part of what can be recognized as the residue of matters taken as food. It is well known that an exclusively animal diet, particularly if the nutritious principles be taken in a concentrated and readily-assimilable form, leaves very little undigested matter to pass into the large intestine, and gives to the fæces a character quite different from that which is observed in herbivorous animals or in man when subjected to an exclusively vegetable diet. The characters of the residue of the digestion of albuminoid substances are not very distinct. As a rule, none of the albuminoids are to be recognized in the healthy fæces by the ordinary tests.

Many insoluble inorganic substances are taken with the food and appear unchanged in the fæces. The fæces of dogs fed exclusively on bones, which were formerly administered internally as a remedy for epilepsy, under the name of *album Græcum*, are composed almost entirely of calcareous matter. With regard to the ordinary inorganic constituents of the fæces, however, it is difficult to say how much is derived from the ingesta and how much from the different intestinal secretions.

Contents of the Large Intestine.

When the contents of the small intestine have passed the ileo-cæcal valve, they become changed in their general character, partly from admixture with the secretions of this portion of the canal, and are then known as the fæces. The most palpable of these changes relate to consistence, color, and odor.

Fæcal matter has a much firmer consistence than the contents of the ileum, which is due to a constant absorption of the liquid portions. As a rule, the consistence is great in proportion to the length of time that the fæces remain in the large intestine; and this is variable in different persons and in the same person, in health, depending somewhat upon the character of the food. The color changes from the yellow, more or less bright, which is observed in the ileum, to the dark yellowish-brown, characteristic of the fæces. Although the bile-pigment cannot usually be recognized by the ordinary tests, it is this which gives to the contents of the large intestine their peculiar color, which is lost when the bile is not discharged into the duodenum. In a specimen of healthy human fæces, which had been dried, extracted with alcohol, the alcoholic solution precipitated with ether, and the precipitate dissolved in distilled water, we failed to detect the slightest trace of the biliary salts by Pettenkofer's test. In a watery extract of the same fæces, the addition of nitric acid also failed to show the reaction of the coloring matter of the bile. The color of the fæces, however, has been found to vary considerably with the diet.

The odor of the fæces, which is characteristic and quite different from that of the contents of the ileum, is somewhat variable and is due in part to the peculiar decomposition of the residue of the food, in part to the decomposition of the bile, and in part to matters secreted by the mucous membrane of the colon and of the glands near the anus.

The entire quantity of fæces in the twenty-four hours was found by Wehsarg to be about 4·6 ounces. This was the mean of seventeen observations; the largest quantity being 10·8 ounces, and the smallest, 2·4 ounces.

The reaction of the fæces is undoubtedly very variable, depending chiefly upon the character of the food. Marcet found the human excrements always alkaline. Wehsarg, on the other hand, found the reaction generally acid, but very frequently, alkaline or neutral.

The first accurate analyses of the fæces were made by Berzelius; but the great advances which have been made in physiological chemistry since that time have enabled later observers to arrive at results much more definite and satisfactory. Marcet has lately discovered a crystallizable substance peculiar to the human fæces; and we have recently shown that probably the most important excrementitious principle discharged by the rectum is derived from the bile and is a peculiar modification of cholesterine. Most of our statements concerning the composition of the fæces in health will be derived from the researches of Wehsarg and of Marcet and from our own observations.

The proportions of water and solid matter in the fæces is variable. Berzelius found, in the healthy human fæces, 73·3 parts of water and 26·7 parts of solid residue. The average of seventeen observations by Wehsarg was precisely the same. In the observations of Wehsarg, the mean quantity of solid matter discharged in the fæces in the twenty-four hours was 463 grains, the extremes being 882·8 grains and 251·6 grains. The proportion of undigested matters in the solid residue was very small, averaging but little more than ten per cent., the mean quantity in the twenty-four hours in ten observations being but 52·5 grains. This was found, however, to be exceedingly variable; the largest quantity being 126·5 grains, and the smallest, 12·5 grains.

Microscopical examination of the fæces reveals the various vegetable and animal structures which we have referred to as escaping the action of the digestive fluids. Wehsarg also found a "finely divided fæcal matter" of indefinite structure, but containing partly disintegrated intestinal epithelium. Crystals of cholesterine were never observed. Whenever the matter is neutral or alkaline, crystals of the ammonio-magnesian phosphate are found. Mucus is also found in variable quantity in the fæces, with desquamated epithelium, and a few leucocytes.

The quantity of inorganic salts in the fæces is not great. In addition to the ammonio-magnesian phosphate, phosphate of magnesia, phosphate of lime, and a small quantity of iron have been found. The chlorides are either absent or are present only in small quantity.

Marcet has pretty generally found in the human fæces a substance possessing the characters of margaric acid, and volatile fatty acids; the latter free, however, from butyric acid. Cystine is mentioned as an occasional constituent of the fæces. He also found a coloring matter, which is probably a modification of biliverdine.

In 1854, Marcet described a new substance in the human fæces, which he called excretine, and an acid called excretoleic acid, which he supposed to be a compound of excretine. These substances and the one which we described in 1862, under the name of stercorine, are, as far as we know, the only principles that have been recognized as characteristic of the normal fæces; and the stercorine we have found to be one of the most distinct and important of the excrementitious principles in the body. The relations of excretine to the process of disassimilation of the tissues have not been so clearly indicated.

Excretine and Excretoleic Acid.—Excretine was obtained by Marcet from the healthy human fæces in the following way: The fæces were first treated with boiling alcohol until nothing more could be extracted. This alcoholic solution was acid and deposited a sediment on cooling. Milk of lime was then added to the solution, producing a yellowish-brown precipitate and leaving the fluid of a clear straw-color. The precipitate was then collected on a filter, dried, afterward agitated with ether and filtered, forming a clear, yellow solution. In from one to three days, beautiful, long, silky crystals of excretine were formed, generally collected into tufts adhering to the sides of the vessel. Examined by the microscope, these were found to consist of acicular, four-sided prisms of variable size. This substance is insoluble in water, slightly soluble in cold alcohol, but is very soluble in ether and in hot alcohol. Its alcoholic solutions are faintly though distinctly alkaline. Its fusing-point is from 203° to 205° Fahr. It may be boiled with potash for hours without undergoing saponification. Apparently, the quantity of excretine contained in the fæces is not very great, as only 12·6 grains were obtained by Marcet from nine evacuations.

We have very little definite information concerning the production of excretine. Marcet examined, on one occasion, the contents of the small intestine of a man that had died of disease of the heart, without finding any excretine. It is probable that this principle is formed in the large intestine, although farther observations are wanting on this point.

The substance called excretoleic acid is very indefinite in its composition and properties. It is described as an olive-colored fatty acid, insoluble in water, non-saponifiable, and very soluble in ether and in hot alcohol. It fuses at from 77° to 79° Fahr.

Stercorine.—This principle, which we discovered in the fæces in 1862, was described by Boudet in 1833, as existing in excessively minute quantity in the serum of the blood, and was called by him seroline. As we found it to be the most abundant and characteristic constituent of the stercoraceous matter, we proposed to call it stercorine; particularly as our researches led us to the opinion that it really does not exist in the serum, but is formed from cholesterine by the processes employed for its extraction.

Stercorine may be extracted in the following way: The fæces are first evaporated to dryness, pulverized, and treated with ether. The ether-extract is then passed through animal charcoal, fresh ether being added until the original quantity of the ether-extract has passed through. It is impossible to decolorize entirely the solution by this process; but it should pass through perfectly clear and of a pale-amber color. The ether is then evaporated, and the residue is extracted with boiling alcohol. This alcoholic solution is evaporated, and the residue is treated with a solution of caustic potash for one or two hours at a temperature a little below the boiling-point, by which all the saponifiable fats are dissolved. The mixture is then largely diluted with water, thrown upon a filter, and is washed until the fluid which passes through is neutral and perfectly clear. The filter is then carefully dried, and the residue is washed out with ether. The ether solution is then evaporated, extracted with boiling alcohol, and the alcoholic solution is evaporated. The residue of this last evaporation is composed of pure stercorine.

When first obtained, stercorine is a clear, slightly amber, oily substance, about the consistence of Canada balsam used in microscopical preparations. In four or five days it begins to show the characteristic crystals. These are few in number at first, but soon the entire mass assumes a crystalline form. In one analysis, we obtained, from seven and a half ounces of normal human fæces (the entire quantity for the twenty-four hours), 10·417 grains of stercorine, the extract consisting of nothing but crystals. This was all the stercorine to be extracted from the regular, daily evacuation of a healthy male twenty-six years of age and weighing about one hundred and sixty pounds. In the absence of other investigations, the daily quantity of this substance excreted may be assumed to be not far from ten grains.

In many regards, stercorine bears a close resemblance to cholesterine. It is neutral, inodorous, and insoluble in water and in a solution of potash. It is soluble in ether and in hot alcohol, but is almost insoluble in cold alcohol. A red color is produced when it is treated with strong sulphuric acid. It may be easily distinguished from cholesterine, however, by the form of its crystals. It fuses at a low temperature, 96·8° Fahr., while cholesterine fuses at 293° Fahr.

Stercorine crystallizes in the form of thin, delicate needles, frequently mixed with clear, rounded globules, which are probably composed of the same substance in a non-crystalline form. When the crystals are of considerable size, the borders near their extremities are split longitudinally for a short distance. The crystals are frequently arranged in bundles, as in Fig. 81, in which they are represented as seen under a $\frac{1}{10}$-inch objective. In Fig. 82, the crystals are represented as seen under a $\frac{1}{6}$-inch objective. These crystals cannot be confounded with excretine, which crystallizes in the form of regular, four-sided prisms, or with the thin rhomboidal or rectangular tablets of cholesterine. They are identical with the crystals of seroline figured by Robin and Verdiel.

There can be no doubt with regard to the origin of the stercorine which exists in the fæces. We have found that, whenever the bile is not discharged into the duodenum, as is probably the case, for a time, in icterus accompanied with clay-colored evacuations, stercorine is not to be discovered in the dejections. In one case of this kind, in which the fæces were subjected to examination, the matters extracted with hot alcohol were entirely dissolved by boiling for fifteen minutes with a solution of potash, showing the

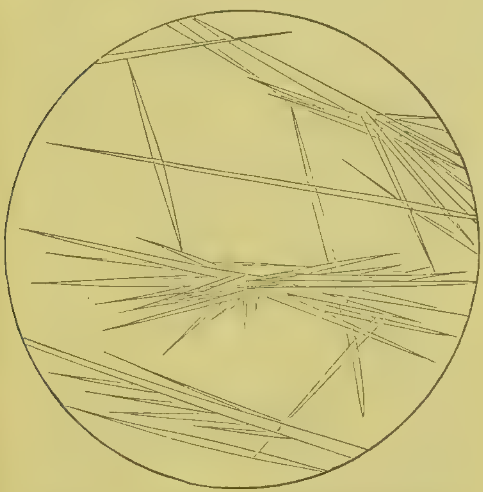


FIG. 81.—*Stercorine from the human fæces.*

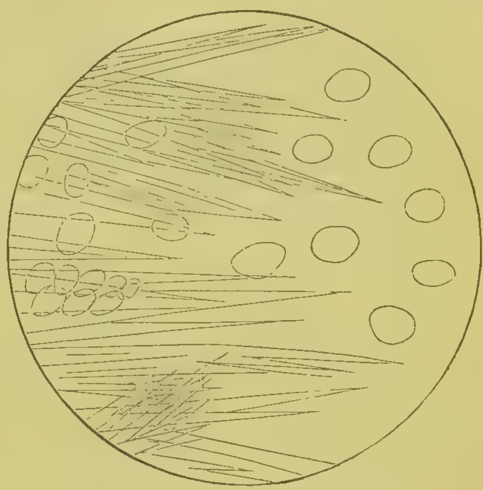


FIG. 82.—*Stercorine from the same specimen after it had been melted, placed upon a glass slide, covered with thin glass, and allowed to crystallize.* The crystallization was very slow, occupying some weeks.

absence of cholesterine and stercorine. In another examination of the fæces from this patient, made nineteen days after, when the icterus had almost entirely disappeared and the evacuations had become normal, stercorine was discovered. These facts show that the cholesterine of the bile, in its passage through the intestine, is changed into stercorine. Both of these principles are crystalline, non-saponifiable, are extracted by the same chemical manipulations, and behave in the same way when treated with sulphuric acid. The stercorine must be regarded as a slight modification of cholesterine, which is the excrementitious principle of the bile.[1]

We have found that the change of cholesterine into stercorine is directly connected with the process of intestinal digestion. If an animal be kept for some days without food, cholesterine will be found in the fæces, although, for a few days, stercorine is also present. It is a fact generally recognized by those who have analyzed the fæces, that cholesterine does not exist in the normal evacuations; but, whenever digestion is arrested, the bile being constantly discharged into the duodenum, cholesterine is found in large quantity. For example, in hibernating animals, cholesterine is always present in the fæces. The same is true of the contents of the intestines during fœtal life; the meconium always

[1] Our researches into the functions of cholesterine have left no doubt that this is an excrementitious principle hardly second in importance to urea. We have found that cholesterine is always more abundant in the blood coming from the brain than in the blood of the general arterial system or in the venous blood from other parts; that its quantity is hardly appreciable in venous blood from the paralyzed side in hemiplegia; and that it is separated from the blood by the liver. We have also shown that, in cases of serious structural disease of the liver accompanied by symptoms pointing to blood-poisoning, cholesterine accumulates in the blood, constituting a condition which we have called cholesteræmia. This subject will be fully discussed under the head of excretion. For a full account of our observations upon the functions of cholesterine, see *The American Journal of the Medical Sciences*, October, 1862.

containing a large quantity of cholesterine, which disappears from the evacuations when the digestive function becomes established.

Movements of the Large Intestine.

Movements of the general character which we have noted in the small intestine occur in the large intestine, although the peculiarities in the arrangement of the muscular fibres and the more solid consistence of the contents render these movements in the large intestine somewhat distinctive. In all instances where the movements have been observed in the human subject or in the lower animals, they have been found to be less vigorous and rapid than the contractions of the small intestine. Indeed, when the abdominal organs are exposed, either in a living animal or immediately after death, movements of the large intestine are generally not observed, except on the application of mechanical or galvanic irritation; and they are then more circumscribed and are much less marked than in any other part of the alimentary canal. In the rabbit, in which the colon is very large, the few spontaneous movements which are sometimes seen on opening the abdomen immediately after death are feeble and irregular, particularly in the cæcum. That the fæces remain for a considerable time in some of the sacculated pouches of the colon, is evident from the appearance which they sometimes present of having been moulded to the shape of the canal. This appearance is frequently observed in the dejections, which are then said to be "figured."

In the cæcum, the pressure of matters received from the ileum forces the mass onward into the ascending colon, and the contractions of its muscular fibres are undoubtedly slight and inefficient. Once in the colon, it is easy to see how the contractions of the muscular structure (the longitudinal bands shortening the canal, and the transverse fibres contracting below and relaxing above) are capable of passing the fæcal mass slowly onward. Although the transverse fibres are thin and seemingly of little power, their contraction is undoubtedly sufficient to empty the sacculi, when assisted by the movements of the longitudinal fibres, especially as the canal is never completely filled and the fæces are frequently in the form of small, moulded lumps. By these slow and gradual movements, the contents of the large intestine are passed toward the sigmoid flexure of the colon, where they are arrested until the period arrives for their final discharge. The time occupied in the passage of the fæces through the ascending, transverse, and descending colon is undoubtedly variable in different persons, as we find great variations in the intervals between the acts of defæcation. During their passage along the colon, the contents of the canal assume more and more of the normal fæcal consistence and odor and become slightly coated with the mucous secretion of the parts.

It has been pretty conclusively shown that the accumulation of fæces generally takes place in the sigmoid flexure of the colon; for, under normal conditions, the rectum is found empty and contracted. This part of the colon is much more movable than other portions and is better calculated as a receptacle for fæces. At certain tolerably regular intervals, the fæcal matter is passed into the rectum and is then almost immediately discharged from the body.

Defæcation.

In health, expulsion of fæcal matters takes place with regularity generally once in the twenty-four hours. This rule, however, is by no means invariable, and dejections may habitually occur twice in the day or every second or third day, within the limits of perfect health. It is well known that habit has a great influence upon the regularity of defæcation; and sometimes, in cases of irregularity, physicians have recommended patients to make an effort to void the fæces at a certain time every day, this practice being frequently followed by the best results. At the time when defæcation ordinarily takes place, a peculiar sensation is experienced calling for an evacuation of the bowels; and, if this be disregarded, the desire may pass away, after a little time, the act becoming impossible. Under these circumstances, it is probable that the fæces are passed out of the rectum by antiperistaltic action.

The condition which immediately precedes the desire for defæcation is probably the descent of the contents of the sigmoid flexure of the colon into the rectum. It was formerly thought that the fæces constantly accumulated in the dilated portion of the rectum, where they remained until an evacuation took place; but the arguments of O'Beirne against such a view are conclusive. He has demonstrated, by numerous explorations in the human subject, that, under ordinary conditions, the rectum is contracted and contains neither fæces nor gas. It is, indeed, a fact familiar to every surgeon, that the rectum usually contains nothing which can be reached by the finger in physical examinations, and that paralysis or section of the muscles which close the anus by no means involves, necessarily, a constant passage of fæcal matter. O'Beirne not only found the rectum empty and presenting a certain amount of resistance to the passage of injected fluids, but, on passing a stomach-tube into the bowel, after penetrating from six to eight inches it passed into a space in which its extremity could be moved with great freedom, and there was instantly a rush of flatus, of fluid fæces, or of both, through the tube. In some instances in which nothing escaped through the tube, the instrument conveyed to the hand an impression of having entered a solid mass; and on being withdrawn it contained solid fæces in its upper portion. According to this observer, the sensation which leads to an effort to discharge the fæces is due to the accumulation of matters in the sigmoid flexure, which finally present at the contracted portion of the rectum just at its commencement. This constriction, situated at the most superior portion of the rectum, is sometimes spoken of as the sphincter of O'Beirne.

The above is undoubtedly the mechanism of the descent of fæcal matter into the rectum in defæcation, as the act is usually performed; but, under certain circumstances, fæces must accumulate in the dilated portion of the rectum. Ordinarily, the discharge of fæces only takes place after the efforts have been continued for a certain time; and when the evacuation is "figured," the whole length discharged frequently exceeds so much the length of the rectum, that it is evident that a portion of it must have come from the colon. O'Beirne states, indeed, that he has frequently examined the rectum at the moment when a moderate inclination to go to stool is felt, and found it empty and contracted. But, in cases in which the fæces are very fluid, or when the call for an evacuation has not been regarded and has become imperative, the immediate discharge of matters when the sphincter is relaxed shows that the rectum has been more or less distended. In many persons of constipated habit, and particularly in old subjects, the rectum may become the seat of large accumulations of hardened and impacted fæces; but this is a pathological condition.

The sensation which ordinarily precedes and gives rise to the evacuation of fæcal matter is peculiar and very variable in intensity. When this sensation is well marked but not excessive, it is probably due to the presence of fæcal matter in the rectum, not in sufficient quantity, however, to press forcibly upon the sphincter. Pressure upon the rectum from any cause, or irritation of its mucous membrane, is apt to give rise to this peculiar sensation to a very marked degree. In some diseases, the exaggeration of this sensation, then called tenesmus, is very distressing.

In the process of defæcation, the first act is the passage, by peristaltic contractions, of the contents of the sigmoid flexure of the colon through the slightly-constricted opening of the rectum into its dilated portion below. The fæcal matter, however, is not allowed to remain in this situation, but it passes into the lower portion of the rectum, in obedience to the contractions of its muscular coat, assisted by the action of the abdominal muscles and the diaphragm. The circular fibres of the rectum undergo the ordinary peristaltic contraction; and the action of the longitudinal fibres is to render the rectum shorter and more nearly straight. The internal and the external sphincter present a certain amount of resistance to the discharge of the fæces, more particularly the external sphincter, which is a striated muscle of considerable power. There is always, however, a voluntary relaxation of this muscle, or rather a cessation of its semi-voluntary contraction, which immediately precedes the expulsive act. The dilatation of the anus is also facilitated by the action of the levator ani, which arises from the posterior surface of the body and ramus of the pubis, the inner surface of the spine of the ischium, and a line of fascia between these two points, passes downward, and is inserted into the median raphe of the perineum and the sides of the rectum, the fibres uniting with those of the sphincter. While this muscle forms a support for the pelvic organs during the act of straining, it steadies the end of the rectum, and, by its contractions, favors the relaxation of the sphincter and draws the anus forward.

The action of the diaphragm and the abdominal muscles is very simple. They merely compress the abdominal organs, and consequently those contained in the pelvis, and assist in the expulsion of the contents of the rectum. The diaphragm is the most important of the voluntary muscles concerned in this process; and, during the act of straining, the lungs are moderately filled and respiration is interrupted. The vigor of these efforts depends greatly upon the consistence of the fæcal mass, very violent contractions being frequently required for the expulsion of hardened fæces after long constipation. Although more or less straining generally takes place, the contractions of the muscular coats of the rectum are frequently competent of themselves to expel the fæces, especially when they are soft. This can be shown by arresting all voluntary muscular action during an easy act of defæcation, when the fæces may be passed by contractions of the rectum alone.

By a combination of the movements above described, the floor of the perineum is pressed outward, the anus is dilated, the sharp bend in the lower part of the rectum is brought more into line with the rest of the canal, and a portion of the contents of the rectum is expelled. Very soon, however, the passage of fæces is interrupted by a contraction of the levator ani and the sphincter, by which the anus is suddenly and rather forcibly retracted. This muscular action may be effected voluntarily; but, after the sphincter has been dilated for a time, the evacuation is interrupted in this way, notwithstanding all efforts to oppose it. After a time, another portion of fæces is discharged, until the matters have ceased to pass out of the sigmoid flexure and the rectum has been emptied. The mucous membrane of the rectum, which is rather loosely held to the subjacent tissue, is slightly prolapsed during an evacuation, but it returns shortly after the act has been completed.

Very little need be said concerning the influence of the nervous system on the movements concerned in defæcation. The non-striated muscular fibres which form the muscular coat of the rectum are supplied with nerves from the sympathetic system; and to the external sphincter are distributed filaments from the last sacral pair of the spinal nerves. These nerves bring the sphincter to a certain degree under the control of the will and impart likewise the property of tonic contraction, by which the anus is kept constantly closed.

Gases found in the Alimentary Canal.

In the human subject, a certain quantity of gas is generally found in the stomach and in the small and large intestine. The most accurate analyses of these gases, as they may be supposed to exist in the human subject in health, are those of Magendie and Chevreul, who had the opportunity of examining the bodies of several criminals immediately after execution.

The gases in the stomach appear to have no definite function. They generally exist in very small quantity, and they are sometimes absent. The oxygen and nitrogen are derived from the little bubbles of air which are incorporated with the alimentary bolus during mastication and insalivation. The other gases are probably evolved from the food during digestion; at least, there is no satisfactory evidence that they are produced in any other way. Magendie and Chevreul collected and analyzed a small quantity of gas from the stomach of an executed criminal a short time after death and ascertained that it had the following composition:

Gases contained in the Stomach.

Oxygen	11·00
Carbonic acid	14·00
Pure hydrogen	3·55
Nitrogen	71·45
	100·00

Magendie and Chevreul found three different gases in the small intestine. Their examinations were made upon three criminals soon after execution. The first was twenty-four years of age, and, two hours before execution, had eaten bread and Gruyère cheese and had drunk red wine and water. The second, who was executed at the same time, was twenty-three years of age, and the conditions as regards digestion were the same. The third was twenty-eight years of age, and, four hours before death, he ate bread, beef, and lentils, and drank red wine and water. The following was the result of the analyses:

Gases contained in the Small Intestine.

	First Criminal.	Second Criminal.	Third Criminal.
Carbonic acid	24·39	40·00	25·00
Pure hydrogen	55·53	51·15	8·40
Nitrogen	20·08	8·85	66·60
	100·00	100·00	100·00

No oxygen was found in either of the examinations, and the quantities of the other gases were so variable as to lead to the supposition that their proportion is not at all definite. We have already alluded to the mechanical function of these gases in intestinal digestion.

In the large intestine, the constitution of the gases presented the same variability as in the small intestine. Carburetted hydrogen was found in all of the analyses. In the large intestine of the first criminal and in the rectum of the third, were found traces of sulphuretted hydrogen. The following is the result of the analyses in the cases just cited. In the third, the gaseous contents of the cæcum and the rectum were analyzed separately:

Gases contained in the Large Intestine.

	First Criminal.	Second Criminal.	Third Criminal. Cæcum.	Third Criminal. Rectum.
Carbonic acid	43·50	70·00	12·50	42·86
Carburetted hydrogen and traces of sulphuretted hydrogen	5·47	.....	.....	.....
Pure hydrogen and carburetted hydrogen	.....	11·60	.....	11·18
Pure hydrogen	.....	.....	7·50	.....
Carburetted hydrogen	.....	.....	12·50	.....
Nitrogen	51·03	18·40	67·50	45·96
	100·00	100·00	100·00	100·00

Origin of the Intestinal Gases.—With our present information on this subject, the most reasonable view to take of the origin of the gases normally found in the intestines is that they are given off from the articles of food in their various stages of digestion and decomposition. That this is the principal source of the intestinal gases, there can be no doubt; and it is well known that certain articles of food, particularly vegetables, generate much more gas than others. The principal gases found in the intestinal canal may all be obtained from the food. Some of them, as hydrogen and carburetted hydrogen, do not exist in the blood; and it is difficult to conceive how they can be generated in the intestine except by decomposition of some of the articles of food. Hydrogen and its compounds are always found in quantity in the small and the large intestine.

It is said that gas is sometimes found in the intestines of the fœtus, and that it may be generated in a loop of intestine in a living animal, after a portion of the canal has been drawn out, isolated by ligatures, freed from its liquid and gaseous contents, and returned to the abdomen. In some diseased conditions, also, it is very common for the abdomen to become rapidly tympanitic, the gas being generated so quickly that its presence is not easily explained by supposing it to be evolved by decomposition of the ingesta. It has, indeed, been supposed that the intestinal mucous membrane is capable of secreting gases as well as liquids; but there do not appear to be any positive facts in support of this view. No doubt some of the gases which may be formed in the intestine are capable of absorption. It is impossible to say, however, that even the gases normally held in solution in the blood, namely, oxygen, nitrogen, and carbonic acid, are exhaled from the blood into the intestinal cavity. Oxygen is never given off in this way, for this gas has been found only in the stomach and is there derived from air which has been swallowed. With regard to the origin of the other gases found in the intestine under the peculiar circumstances just mentioned, in which they are apparently generated with much rapidity, there are not sufficient data to enable us to form an intelligent opinion.

CHAPTER X.

ABSORPTION—LYMPH AND CHYLE.

General considerations of absorption—Absorption by blood-vessels—Absorption by lacteal and lymphatic vessels—Physiological anatomy of the lacteal and lymphatic system—Absorption by the lacteals—Absorption from parts not connected with the digestive system—Absorption of fats and insoluble substances—Variations and modifications of absorption—Imbibition and endosmosis—Imbibition by animal tissues—Mechanism of the passage of liquids through membranes—Capillary attraction—Endosmosis through porous septa—Endosmosis through animal membranes—Endosmosis through liquid septa—Diffusion of liquids—Endosmotic equivalents—Modifications of endosmosis—Application of physical laws to the function of absorption—Transudation—Lymph and chyle—Mode of obtaining lymph—Quantity of lymph—Properties and composition of lymph—Alterations of the lymph—Corpuscular elements of the lymph—Leucocytes—Development of leucocytes in the lymph and chyle—Globulins—Origin and function of the lymph—General properties of the chyle—Composition of the chyle—Comparative analyses of the lymph and the chyle—Microscopical characters of the chyle—Movement of the lymph and chyle.

Digestion has two great objects: one is to liquefy the different alimentary principles; and the other, to commence the series of transformations by which these principles are rendered capable of nourishing the organism. The principles thus acted upon are taken into the blood as fast as the requisite changes in their constitution are effected; and, once received into the circulation, they become part of the great nutritive fluid, supplying the waste which the constant regeneration of the tissues from materials furnished by the blood necessarily involves. The only group of principles which possibly does not obey this general law is the fats. Although a small portion of the fat taken as food passes directly into the blood-vessels of the intestinal canal, by far the greatest part finds its way into the circulation by means of special absorbent vessels which empty into large veins. In whatever way fat enters the blood, it is never dissolved, but is reduced to the condition of a fine emulsion.

The process by which digested materials are taken into the blood is called absorption. It is now recognized that two sets of vessels are concerned in the performance of this function; namely, the blood-vessels and the lacteals. Those parts of the food which have been rendered fluid and are capable of forming a homogeneous mixture with the blood-plasma are absorbed chiefly by the blood-vessels, although a small portion finds its way into the lacteals. The emulsified fats are taken up in greatest part by the lacteals, although a small quantity is taken directly into the blood. In treating of this subject, it will be convenient to consider separately the action of these two kinds of vessels.

Absorption by Blood-Vessels.

That soluble substances can pass through the delicate walls of the capillaries and small veins and that absorption actually takes place in great part by blood-vessels, are facts which hardly demand discussion at the present day. Soluble principles which have disappeared from the alimentary canal have been repeatedly found in the blood coming from this part, even when the lymphatics have been divided and communication existed only through the blood-vessels. The old theoretical view which was entertained before the lymphatics and lacteals were discovered was that absorption took place by blood-vessels; but, after special absorbent vessels had been described, it was generally supposed that they furnished the only avenue for the entrance of new matters into the economy, although the doctrine of vascular absorption was retained by a few. It was only after the conclusive experiments of Magendie, in 1809, that positive proof was given of the absorbing power of the blood-vessels. These experiments settled the question of vascular absorption, although they led some to take too exclusive a view of the importance of the venous radicles in this function and to deny that absorption took place to any considerable extent through the lymphatic and the lacteal system. At the present day, there is no difference of opinion among physiologists concerning the direct absorption of nutritive matters by the blood-vessels of the alimentary canal. It has been repeatedly shown, indeed, that, during absorption, the blood of the portal vein is rich in albuminoids, sugar, and in other principles resulting from digestion.

In the mouth and œsophagus, the sojourn of alimentary principles is so brief and the changes which they undergo so slight, that no absorption of any moment can take place. It is evident, however, that the mucous membrane of the mouth is capable of absorbing certain soluble matters, from the effects which are constantly observed when the smoke or the juice of tobacco is retained in the mouth, even for a short time. In the stomach, however, the absorption of certain materials takes place with great activity. A large proportion of the ingested liquids and of those principles of food which are dissolved by the gastric juice and converted into albuminose is taken up directly by the blood-vessels of the stomach. It may, indeed, be assumed, as a general law, that digested matters are in great part absorbed as soon as their transformations in the alimentary canal have been completed.

In the passage of the food down the intestinal canal, as we have already seen, there is a constant loss of material. As the digestion of the albuminoids is completed, these principles are absorbed, and their passage into the mass of blood is indicated chiefly by an increase in its proportion of albuminoid constituents. Many of the other products of digestion, such as glucose and fatty emulsion, have also been demonstrated in quantity in the blood of the portal vein during absorption. The fats, though taken up in greatest part by the lacteals, are always found in greater or less quantity in the portal blood. It has frequently been observed that, after a full meal consisting largely of fat, the blood from the portal vein, as it cools and coagulates, leaves a white scum of fat upon the surface. On one occasion, we observed, in the portal blood of an animal killed in full digestion, a layer of fat on cooling so thick that a quantity of blood, which was spilled upon a table and the floor, was white, like milk. We have since frequently attempted to demonstrate this excessively chylous condition of the blood during the absorption of fats, but have found that it is not generally so well marked.

The greatest part of the food is absorbed by the intestinal mucous membrane, and, with the alimentary substances proper, a large quantity of secreted fluid is reabsorbed. This fact is particularly striking as regards the bile. The biliary salts disappear as the alimentary mass passes down the intestine and are undoubtedly absorbed, although they are so changed that they cannot be detected in the blood by the ordinary tests. In this portion of the alimentary canal, it will be remembered that an immense absorbing surface is provided, by the arrangement of the mucous membrane in folds, forming the valvulæ conniventes, and by the presence of the innumerable villi which are found throughout the small intestine. A certain portion of the gaseous contents of the intestines is also absorbed, although it is not easily ascertained what particular gases are thus taken up.

Absorption by Lacteal and Lymphatic Vessels.

The history of the discovery of what is ordinarily termed the absorbent system of vessels, from the vague allusions of Hippocrates, Galen, Aristotle, and others, to the description of the thoracic duct in the middle of the sixteenth century, by Eustachius, and finally to the discovery of the lacteals by Asellius, in 1622, is more interesting in an anatomical than in a physiological point of view. Our knowledge of the anatomy of the absorbent system dates from the discovery of the thoracic duct; but, from the discovery of the lacteals by Asellius, dates the history of these vessels as the carriers of nutritive matters from the intestinal canal to the general system.

In 1649, Pecquet discovered the receptaculum chyli and demonstrated that the lacteals did not pass to the liver, but emptied the chyle into the commencement of the thoracic duct, by which it was finally conveyed into the venous system. In 1650–'51, the anatomical history of the absorbent vessels was completed by the discovery, by Rudbeck, of vessels carrying a colorless fluid, in the liver and finally in almost all parts of the body. Rudbeck demonstrated the anatomical identity of these vessels with the lacteals. They were afterward carefully studied by Bartholinus, who gave them the name of lymphatics. It is unnecessary to follow out the various researches made into the structure of the lymphatics in man and the inferior animals by the Hunters, Hewson, Monro, Cruikshank, and other of the older anatomists and physiologists.

The old idea, which dates from the discoveries of Asellius and Pecquet, that the lacteals absorb all the products of digestion, was overthrown by the experiments of Magendie and of those who experimented after him upon vascular absorption. It is now known that the fatty portions of the food, reduced to a very fine emulsion by the pancreatic juice, are absorbed by this system of vessels, and that these are the only principles which are taken up in great quantity. The arguments which we have already mentioned are sufficient to establish this fact. If the abdomen of a living animal be opened during full digestion, then, and then only, will the lacteals and the thoracic duct be found distended with fatty emulsion. If the organ which digests fat be rendered incapable of performing its function, the lacteals cease to carry chyle. These vessels do not appear in the mesentery until the food has passed the orifice of the pancreatic duct. Finally, the observations of Bouchardat and Sandras remove all doubt as to the absorption of the products of the digestion of fatty matters by the lacteals; for these observers found not only that in dogs the proportion of fat in the chyle was increased *pari passu* with an increase in the quantity of fat taken as food, but that the particular kinds of fat administered to the animals could be recognized in the chyle. We have seen that a certain quantity of fat escapes the lacteals and is absorbed directly by the blood-vessels; and it becomes an important question to determine whether the lacteals, in addition to their more prominent function, be not concerned in the absorption of drinks, the albuminoids, saline and saccharine matters, etc. This question will be taken up after a consideration of certain points in the anatomy of the lymphatic system.

Physiological Anatomy of the Lacteal and Lymphatic System.—One of the most difficult problems in anatomy is to determine the situation and mode of origin of the lymphatics in different parts of the body. The tenuity of the walls of these vessels, even in their course, and the presence of innumerable valves, render it impossible to study them by the ordinary methods of injection. Since it has been ascertained, however, that they originate in many parts by a rich, anastomosing plexus, their anatomy has been well made out in certain situations by simply puncturing with a fine-pointed canula the parts in which the plexus is supposed to exist, and allowing a fluid, generally mercury, to gently diffuse itself in the vessels of origin. Following the course of the vessels, the fluid passes into the larger trunks and thence to the lymphatic glands. The regularity of the plexus through which the fluid is first diffused and the passage of the injection through the larger vessels to the glands are positive proof that the lymphatics have been penetrated and that the appearances observed are not the result of mere infiltration.

By the method of investigation above indicated, we may recognize the superficial vessels of the skin, deeper vessels situated just beneath the skin, and vessels in the serous membranes, glandular organs, lungs, tendons, etc., in addition to the larger trunks, such as the thoracic duct. The lacteal system presents essentially the same characters as the general lymphatics, and the vessels are filled with colorless lymph during the intervals of digestion. In many situations, the lymphatics present in their course little, solid structures called lymphatic glands.

The mode of origin of the finest vessels, in the lymphatic radicles, is exceedingly obscure, notwithstanding the numerous investigations which have been made within the last few years, particularly by German anatomists. We shall first describe, however, the mode of origin of what may be called the true vessels, in those parts in which the results of anatomical study seem positive and definite, before we discuss the various theories which have been proposed to account for certain of the phenomena of absorption.

Lymphatics have not been actually injected and demonstrated in all the tissues of the body; but, in some parts in which it has been thus far impossible to inject them, we are not justified in assuming positively that they do not exist. For example, in the intestinal villi, according to Sappey, these vessels have never been seen, although their existence is almost certain. The most generally received view with regard to the ordinary mode of origin of the lymphatic vessels is that they commence by a capillary plexus, which does not communicate with either the small arteries, veins, or the capillary blood-vessels, and is generally situated external to the blood-vessels. It does not appear that the vessels composing this plexus vary much in size. They are very elastic, and, after distention by injection, they return to a very small diameter when the fluid is allowed to escape. It is probable, therefore, that the capacity of the vessels is much exaggerated by the means which are taken to render them apparent. In the elaborate observations by Dr. Belaieff, of St. Petersburg, into the origin of the lymphatics of the penis, the walls of the vessels were rendered apparent by the action of nitrate of silver in solution in pure water, and it is probable that they were very little distended. The smallest of these vessels had a diameter of about $\frac{1}{300}$ of an inch. This may be taken as their average diameter in the primitive plexus. This plexus, when the vessels are abundant, as they are in certain parts of the cutaneous surface, resembles an ordinary plexus of capillary blood-vessels, except that the walls of the vessels are thinner and their diameter is greater.

The smallest lymphatic vessels are by far the most numerous. They are arranged in the form of a fine plexus, very superficially situated in the skin. A second plexus exists just beneath the skin, composed of vessels of much greater diameter. The skin is thus enclosed, as it were, between two plexuses of capillary lymphatics. A plexus analogous to the most superficial plexus of the skin is found just beneath the surface of the mucous membranes. These may, indeed, be classed with the superficial lymphatics. The deep lymphatics are much larger and less numerous, and their origin is less easily made out.

These accompany the deeper veins in their course. They receive the lymph from the superficial vessels.

No valvular arrangement is found in the smallest lymphatics; but the vessels coming from the primitive plexuses, as well as the large vessels, contain valves in immense numbers. These valves, being so closely set in the vessels, give to them, when filled with injection, a peculiar and characteristic beaded appearance.

FIG. 83.—*Superficial lymphatics of the skin of the palmar surface of the finger.* (Sappey.)

FIG. 84.—*Deep lymphatics of the skin of the finger.* (Sappey.)
1, 1, deep net-work of cutaneous lymphatics; 2, 2, 2, 2, lymphatic trunks connected with this net-work.

FIG. 85.—*Same finger, lateral view, showing lymphatic trunks connected with the superficial net-work.* (Sappey.)

The course of the lymphatics is generally tolerably direct. As they pass toward the great trunks by which they communicate with the venous system, they present a peculiar anastomosis with the adjacent vessels, called anastomosis by bifurcation; that is, as a vessel passes along with other vessels nearly parallel with it, it bifurcates, and the two branches pass into the nearest vessels on either side. These anastomoses are quite frequent, and they generally occur between vessels of equal size. In their course, the vessels pass through the lymphatic glands, which will be described farther on.

A notable peculiarity in the lymphatic vessels is that they vary very little in size, being nearly as large at the extremities as they are near the trunk. In their course, they are always much smaller than the veins and do not progressively enlarge as they pass on to the great lymphatic trunks. The largest-sized vessels as they pass from the skin are from $\frac{1}{25}$ to $\frac{1}{12}$ of an inch in diameter, and the larger vessels, in their course, have a diameter of from $\frac{1}{12}$ to $\frac{1}{8}$ of an inch. As in the case of the smallest lymphatics in the primitive plexus, the elasticity of the walls of the vessels renders their caliber greatly dependent upon the pressure of fluid in their interior. Many anatomists have noticed that vessels, which are hardly perceptible while empty, are capable of being dilated to the diameter of half a line or more, returning to their original size as soon as the distending fluid is removed.

The peculiarities which the lymphatics present in the different tissues and organs do not possess much physiological interest, except the arrangement of the vessels of origin in the substance of the brain and spinal cord. In the skin, the only interesting peculiarity which we have not already noticed is that the vessels appear to be very unequally distributed in different parts of the surface. According to Sappey, they are particularly

FIG. 86.—*Superficial lymphatics of the arm.* (Sappey.)

FIG. 87.—*Superficial lymphatics of the leg.* (Sappey.)

abundant in the scalp over the biparietal suture, the soles of the feet and the palms of the hand, the fingers at the lateral portion of the last phalanges, and the scrotum. In the median portion of the scrotum, they attain their highest degree of development. They are also found, though in less number, originating from around the median line on the anterior and posterior surface of the trunk, the posterior median portion of the extremities, the skin over the mammæ, and around the orifices of the mucous passages. Sappey has injected lymphatic vessels in the anterior portion of the forearm, the thigh, and the leg, and the middle portion of the face, although they are demonstrated with difficulty in these situations. If they exist at all in other portions of the cutaneous surface, they are not numerous and are rudimentary.

In the mucous system the lymphatics are very abundant. Here are found, as in the skin, two distinct layers which enclose between them the whole thickness of the mucous membrane. The more superficial of these layers is composed of a rich plexus of small vessels, and, beneath the mucous membrane, is a plexus consisting of vessels of larger size and less numerous. The superficial plexus is exceedingly rich in the mixed structure which forms the lips and the glans penis, and around the orifices of the mouth, the nares, the vagina, and the anus. There are certain mucous membranes in which the lymphatics have never been injected. In the serous membranes, the lymphatics have been demonstrated in great abundance. Lymphatics have been demonstrated taking their origin in the voluntary muscles, the diaphragm, the heart, and the non-striated muscular coats of the hollow viscera, although their investigation in these situations is exceedingly difficult.

Lymphatics are found coming from the lungs in immense numbers. These arise in the walls of the air-cells and surround each pulmonary lobule with a close plexus. The deep vessels follow the course of the bronchial tubes, passing through the bronchial glands and the glands of the bifurcation of the trachea, to empty into the thoracic duct and the great lymphatic duct of the right side.

In the glandular system, including the ductless glands, and in the ovaries, the lymphatic vessels are, as a rule, more abundant than in any other parts of the body. They are especially numerous in the testicle, the ovary, the liver, and the kidney.

In the substance of the brain and spinal cord, Robin and His have demonstrated a curious system of vessels which entirely surround the capillary blood-vessels and are connected with the lymphatic trunks or reservoirs described by Fohmann under the pia mater. The capillary blood-vessels thus float in a fluid contained in these cylindrical sheaths, which exceed them in diameter by from $\frac{1}{1250}$ to $\frac{1}{400}$ of an inch. These investing vessels follow the blood-vessels in their ramifications, and contain a clear fluid, with bodies resembling the lymph-corpuscles. When Robin first described these vessels minutely, he did not state definitely their physiological relations; but he has since published a memoir in which he describes them as true lymphatic vessels, analogous to the lymphatics which partly surround the small blood-vessels in fishes, reptiles, and batrachians. In these animals, the lymphatics in many parts nearly surround the blood-vessels, to the walls of which the edges of their proper coat are adherent; and that portion of the wall of the blood-vessel which is thus enclosed forms at the same time the wall of the lymphatic. This disposition of the lymphatics in the brain and spinal cord would allow of free interchange, by endosmosis and exosmosis, of the liquid portions of the blood and the lymph.

The lymphatic vessels from the superficial and deep portions of the head and face on the right side, and those from the superficial and deep portions of the right arm, the right half of the chest, and the mammary gland, with a few vessels from the lungs, pass into the great lymphatic duct (ductus lymphaticus dexter), which empties into the venous system at the junction of the right subclavian with the internal jugular. This vessel is about an inch in length and from one-twelfth to one-eighth of an inch in diameter. It is provided with a pair of semilunar valves at its opening into the veins, which effectually prevent the ingress of blood.

The vessels from the inferior extremities, and those from the lower portions of the trunk, the pelvic viscera, and the abdominal organs, generally pass into the thoracic duct. In their course, all of the lymphatics pass through the small, flattened, oval bodies, called the lymphatic glands, which are so abundant in the groin, the axilla, the pelvis, and in some other parts. From two to six vessels, called the vasa afferentia, enter these bodies, having first broken up into a number of smaller vessels just before they pass in. They pass out by a number of small vessels which unite to form one, two, or three trunks, generally of larger size than the vasa afferentia. The vessels which thus emerge from the glands are called vasa efferentia.

The lymphatics of the small intestine, called lacteals, pass from the intestine between the folds of the mesentery to empty, sometimes by one, and sometimes by four or five trunks, into the receptaculum chyli. In their course, the lacteals pass through several sets of lymphatic glands, which are here called mesenteric glands.

The thoracic duct, into which the great majority of the lymphatic vessels empty, is

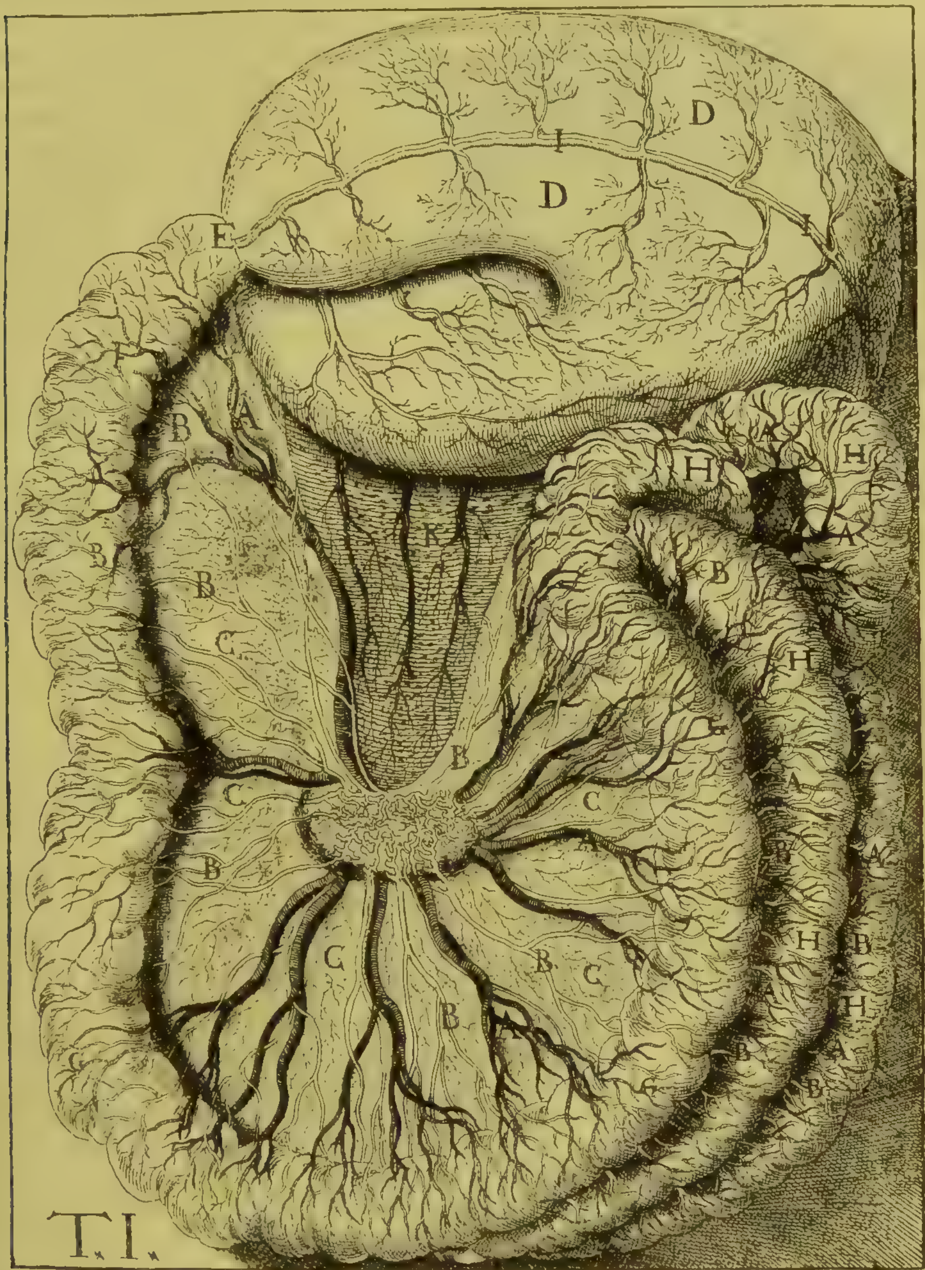


Fig. 88.—*Stomach, intestine, and mesentery, with the mesenteric blood-vessels and lacteals.* (Copied and slightly reduced from a figure in the original work of Asellius, published in 1628.)

A, A, A, A, A, mesenteric arteries and veins; B, B, B, B, B, B, B. B, B, B, lacteals; C, C, C, C, mesentery; D, D, stomach; E, pyloric portion of the stomach; F, duodenum; G, G, G, jejunum; H, H, H, H, H, ileum; I, artery and vein on the fundus of the stomach; K, portion of the omentum.

a vessel with exceedingly delicate walls and about the size of a goose-quill. It commences by a dilatation, more or less marked, called the receptaculum chyli. This is situated upon the second lumbar vertebra. The canal passes upward in the median line for the inferior half of its length. It then inclines to the left side, forms a semicircular curve something like the arch of the aorta, and empties at the junction of the left subclavian with the internal jugular vein. It diminishes in size from the receptaculum to its middle portion and becomes larger again near its termination. It occasionally bifurcates near the middle of the thorax, but the branches become re-united a short distance above. At its opening into the venous system, there is generally a valvular fold, but, according to Sappey, this is not constant. There is always, however, a pair of semilunar valves in the duct, from three-quarters of an inch to an inch from its termination, which effectually prevent the entrance of blood from the venous system.

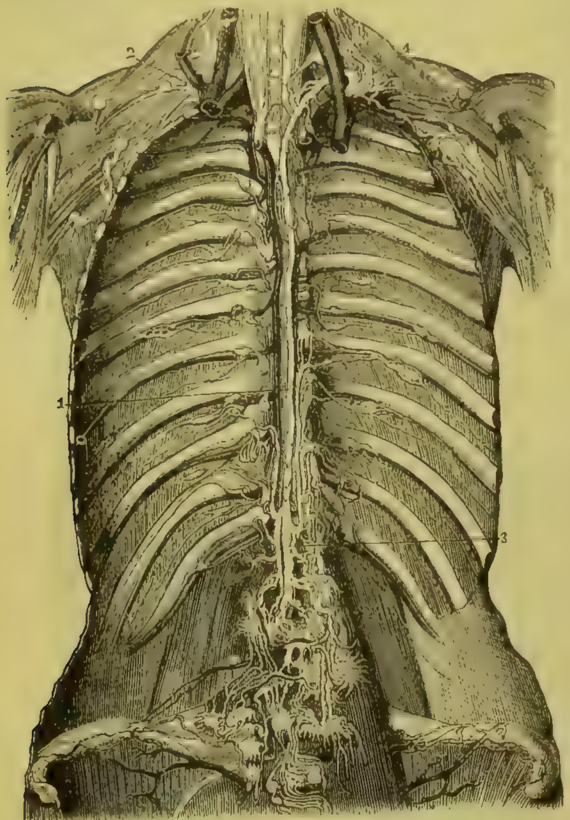


Fig. 89.—*Thoracic duct.* (Mascagni.)
1, thoracic duct; 2, great lymphatic duct; 3, receptaculum chyli; 4, curve of the thoracic duct just before it empties into the venous system.

It is probable that the lymphatic and lacteal vessels have no direct connection with the blood-vessels, except by the two openings by which they discharge their contents into the venous system. The foregoing sketch of the descriptive anatomy of what has been called the absorbent system of vessels shows that they may collect fluids, not only from the intestinal canal during digestion, but from nearly every tissue and organ in the body, and that these fluids are received into the venous circulation.

Structure of the Lacteal and Lymphatic Vessels.—The lymphatic vessels, even those of largest size, are remarkable for the delicacy and transparency of their walls. This is well illustrated in the case of the lacteals, which are hardly visible in the transparent mesentery, unless they be filled with opaque chyle.

From the difficulty in studying the lymphatics at their origin, except by means of injections or by reagents which stain the vessels, investigations into the structure of the smallest vessels have been very few and are not very satisfactory. It is supposed, however, that the vessels here consist of a single amorphous coat, resembling, in this regard, the capillary blood-vessels. Dr. Belaieff describes, in the capillary lymphatics of the penis, a lining of epithelial cells arranged in a single layer. These cells are oval, polygonal, fusiform or dentated, with their long diameter in the direction of the axis of the vessels.

In all but the capillary lymphatics, although the walls are excessively thin, three distinct coats can be distinguished. The internal coat consists of an elastic membrane lined with oblong epithelial cells. This coat readily gives way when the vessels are forcibly distended. The middle coat is composed of longitudinal fibres of the white fibrous tissue, with delicate elastic fibres and unstriped muscular fibres arranged transversely. The external coat is composed of the same structures as the middle coat; but the fibres are arranged, for the most part, longitudinally. In this coat, the muscular fibres do not form a continuous sheet, but are collected into separate fasciculi, which have a direction either longitudinal or oblique. The fibres of connective tissue are very abundant and loosely unite the vessels to the surrounding parts. The internal and the middle coat are closely adherent to each other; but the external coat may readily be separated from the others. Blood-vessels have been found in the walls of the lymphatics, but, as yet, the presence of nerves has not been demonstrated.

The walls of the lymphatic vessels are very closely adherent to the surrounding tissues; so closely, indeed, that even a small portion of a vessel is detached with great difficulty, and the vessels, even those of large size, cannot be followed out and isolated for any considerable distance.

In all the lymphatic vessels, beginning a short distance from their plexus of origin, are found numerous semilunar valves, generally arranged in pairs, with their concavities looking toward the larger trunks. These folds are formed of the inner two coats; but the fold formed of the lining membrane is by far the wider, so that the free edges of the valves are considerably thinner than that portion which is attached directly to the vessel. In some of the vessels, at the point where one lymphatic communicates with another, there is a valve formed of two folds, one of which is much wider than the other; but, in the valves situated in the course of the vessels, the curtains are of about equal size. The valves are very numerous in all of the lymphatics, but they are most abundant in the superficial vessels. The distance between the valves is from one-twelfth to one-eighth of an inch, near the origin of the vessels, and from one-quarter to one-third of an inch, in their course. In the lymphatics situated between the muscles, the valves are less numerous. They are always relatively few in the vessels of the head and neck and in all that have a direction from above downward. Although there are a number of valves in the thoracic duct, they are not so numerous here as in the smaller vessels.


FIG. 90.—*Valves of the lymphatics.* (Sappey.)

In their anatomy and general properties, the lymphatics bear a close resemblance to the veins. Although much thinner and more transparent, their coats have nearly the same arrangement. The arrangement of valves is entirely the same; and, in both systems, the folds prevent the reflux of fluids when the vessels are subjected to pressure. A number of forces (which will be considered hereafter) combine to produce the flow of lymph and chyle in the absorbent system. Among these is intermittent pressure from surrounding parts, which could only operate favorably in vessels provided with numerous valves.

We have already referred to the great elasticity of the lymphatics. It is now pretty generally admitted that the larger vessels and those of medium size are endowed also with contractility, although the action of their muscular fibres, like that of all fibres of the involuntary or non-striated variety, is slow and gradual. Todd and Bowman have demonstrated this property by mechanically irritating the thoracic duct in an animal recently killed, but they observed that the contraction was very slow. Milne-Edwards, quoting from a manuscript presented by Colin to the Academy of Sciences, in 1858, states that this observer noted alternate filling and emptying of some of the lacteal vessels in the mesentery of the ox; portions of the vessels becoming alternately enlarged in the form of pouches, and contracted so that they almost disappeared. There can be no doubt that the lymphatic vessels possess a certain degree of contractility, which is fully as marked, perhaps, as in the venous system.

One of the most important points in connection with the physiological anatomy of the lymphatic vessels, and one, indeed, upon which rest our ideas of the mechanism of absorption by these vessels, is the question of the existence of orifices in their walls, which might allow the passage of solid particles or emulsions. The most recent observations have indicated the probable existence of stomata, of variable size and irregular shape, in the smallest vessels; but it must be acknowledged that one of the strongest arguments in favor of the existence of these orifices is, not their anatomical demonstration, but the fact of the actual passage, through the walls of the vessels, of fatty particles, the entrance of which cannot be explained by the well-known laws of endosmosis. The anatomical evidence of the existence of openings is derived mainly from preparations stained with nitrate of silver. It is assumed that nitrate of silver stains the solid parts of tissues and the borders of the epithelial cells, and that areas which do not present any staining are necessarily open. If this be true, and this view is now very generally accepted, we may consider the existence of openings in the lymphatic vessels as demonstrated. In preparations of the lymphatics, the solution of silver is seen staining the tissues and the borders of the epithelial cells lining the vessels; but there are areas between these cells where no staining is observed and in which no nuclei are brought on by staining with carmine. It is not impossible, however, that the solutions used may fail to attack all parts of the tissue, and that these colorless areas may be closed by an amorphous membrane.

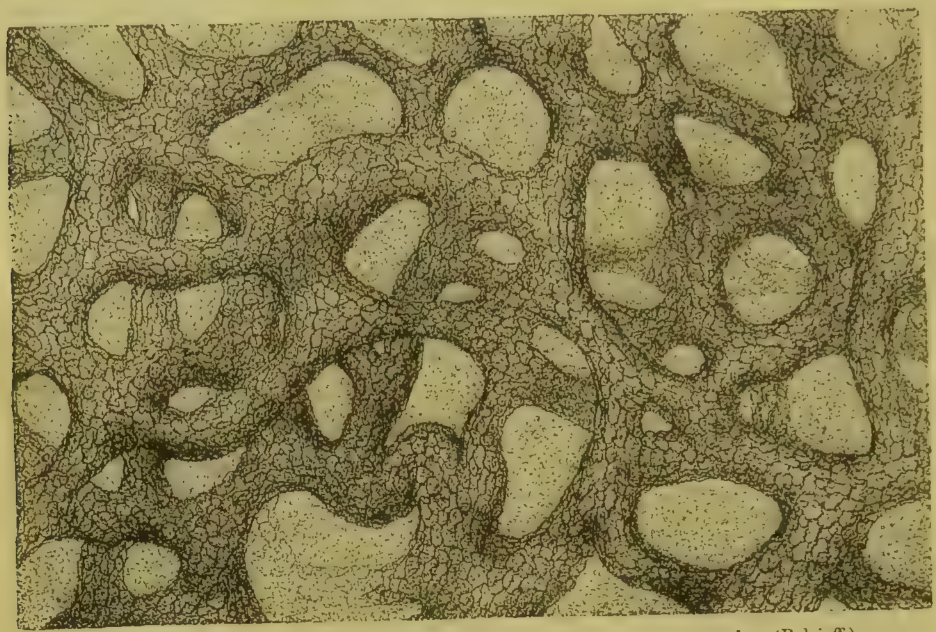


FIG. 91.—*Lymphatic plexus, showing the epithelial lining of the vessels.* (Belaieff.)

With regard to the origin of the lymphatics in the tissues, it does not seem that our actual knowledge extends beyond the small vessels, such as are observed in the superficial net-work of the skin. Within the last few years, Recklinghausen and others have assumed the existence, in the connective tissue (which is so widely distributed in the organism), of minute tubes or canaliculi, which open into the lymphatic vessels, and that these are the true vessels of origin of a great part of the lymphatic system. These little vessels are called serous canaliculi. This view, however, is not sustained by positive demonstration and must be regarded as purely hypothetical; and the same may be said of the opinion advanced by some that the lymphatics originate in lacunæ or spaces in the connective tissue or in a system of canals formed by connective-tissue corpuscles and fibres. Sappey asserts very emphatically that not one lymphatic vessel has ever been demonstrated as arising from the substance of connective tissue; and a careful study of recent observations in Germany shows this to be the fact.

Lymphatic Glands.—In the course of the lymphatic vessels, are found numerous small, lenticular bodies, called lymphatic glands. The number of these glands is very great, although it is estimated with difficulty, from the fact that many of them are very small and are consequently liable to escape observation. It may be stated as an approximation that there are from six hundred to seven hundred lymphatic glands in the body. Their size and form are also very variable within the limits of health. They are generally flattened and lenticular, some as large as a bean, and others as small as a small pea or even a pin's-head. They are arranged in two sets; one superficial, corresponding with the superficial lymphatic vessels, and a deep set, corresponding with the deep vessels. The superficial glands are most numerous in the folds at the flexures of the great joints and about the great vessels of the head and neck. The deep-seated glands are most numerous around the vessels coming from the great glandular viscera. A distinct set of large glands is found connected with the lymphatic vessels between the folds of the mesentery. These are known as the mesenteric glands. All of the lymphatic vessels pass through glands before they arrive at the great lymphatic trunks, and most of them pass through several glands in their course.

FIG. 92.—*Lymphatics and lymphatic glands.* (Sappey.)
1, upper extremity of the thoracic duct, passing behind the internal jugular vein; 2, opening of the thoracic duct into the internal jugular and left subclavian vein. The lymphatic glands are seen in the course of the vessels.

There is some difference of opinion among anatomists concerning the intimate structure of the lymphatic glands. Some regard them as composed simply of a plexus of lymphatic vessels, held together by a delicate stroma of fibrous tissue; while others deny that there is any direct communication between the afferent and the efferent vessels, assuming that the vessels which penetrate the glands break up into small branches which open into a parenchyma filled with closed follicles, and that the fluids are collected from the glands by a second set of capillaries connected with the efferent lymphatics. According to the latter view, the mesenteric glands are little more than collections of follicles like the solitary glands of the intestines, held together by a delicate fibrous structure. This difference of opinion seems to be due to the different methods which have been employed in studying the structure of the glands. Taking, for example, the results arrived at by two prominent investigators, Sappey, who has studied these organs with great success by injections, seems to have clearly demonstrated a lymphatic plexus in their interior, while Kölliker, whose investigations have been confined chiefly to examinations of the organs in a recent state, has not been able to follow out the lymphatic vessels, but has accurately described the contents of the alveoli, or what are regarded by others as closed follicles. In attempting to represent what has been actually demonstrated concerning the structure of these bodies, we shall first take up the appearances which are observed in the fresh structures, and afterward, those points which have been demonstrated by minute injections.

The perfect, healthy glands are of a grayish-white or reddish color, of about the consistence of the liver, presenting a hilum where the larger blood-vessels enter and the efferent vessels emerge, and covered, except at the hilum, with rather a delicate membrane, composed of inelastic, with a few elastic fibres. Their exterior is somewhat tuberculated, from the projections of the follicles just beneath the investing membrane. The interior of the glands is soft and pulpy. It presents a coarsely-granular cortical substance, of a reddish-white or gray color, which is from one-sixth to one-fourth of an inch in thickness in the largest glands. The medullary portion, which comes to the surface at the hilum, is lighter colored and coarser than the cortical substance. Throughout the gland, are found delicate fasciculi of fibrous tissue connected with the investing membrane, which serve as a fibrous skeleton for the gland and divide its substance into little alveoli. The structure is far more delicate in the cortical than in the medullary portion.

Within the alveoli, are irregularly-oval, closed follicles, about $\frac{1}{250}$ of an inch in diameter, filled with a fluid and with cells like those contained in the solitary glands of the intestines and the patches of Peyer. These follicles do not seem to occupy the medullary portion of the glands, which, according to Kölliker, is composed chiefly of a net-work of lymphatic capillaries, mixed with rather coarse bands of fibrous tissue. The follicular structures in the lymphatic glands resemble the closed follicles in the mucous membrane of the intestinal canal and the Malpighian bodies of the spleen.

The elaborate researches of Sappey leave scarcely any doubt as to the course and arrangement of the lymphatic vessels in the interior of the lymphatic glands, although the view advanced by him that these bodies consist mainly of lymphatics with a little fibrous tissue cannot be sustained. By pricking a perfectly healthy gland with the delicate point of his apparatus for injecting the lymphatics, he has seen the mercury successively fill the different capillary vessels and pass into the vasa efferentia. Sappey does not appear, however, to have caused the injection to pass from the afferent to the efferent vessels, entirely through this plexus; and, while the fact of the continuity of these vessels through a capillary plexus is extremely probable, it has not, as yet, been positively proven.

As far as has been ascertained, the following is the course of the lymphatic vessels through the glands: From two to six vasa afferentia approach the gland, and, when within about a quarter of an inch of it, they break up into numerous small branches which penetrate its investing membrane. In the substance of the gland, these vessels are distributed in the capillary plexus just described and emerge by the vasa efferentia, which are always larger than the afferent vessels and are from one to three in number. In attempting to pass injections entirely through the glands, the fluid has frequently been observed to pass into the small veins; so that some anatomists have assumed that there is a connection in the substance of the glands between the lymphatics and the blood-vessels. It is altogether probable that the passage of fluids into the veins under these circumstances is due to rupture of the vessels; and, at all events, the direct connection between them and the lymphatics has never been satisfactorily demonstrated.

The lymphatic glands are supplied with blood by sometimes one, but generally by several small arteries, which penetrate at the hilum. These vessels pass directly to the medullary portion and there break up into several coarse branches, to be distributed to the cortical substance, where they ramify in an exceedingly delicate capillary net-work, with rather wide meshes, in the closed follicles found in this portion of the gland. This capillary plexus also receives branches from small arterial twigs which penetrate the capsule of the gland at different points. Returning on themselves in loops, the vessels unite to form one or more large veins, which generally emerge at the hilum.

Very little is known regarding the distribution of nerves in the lymphatic glands. A few filaments from the sympathetic system enter with the arteries, but they have never been traced to their final distribution. The entrance of filaments from the cerebro-spinal system has never been demonstrated.

It is evident, from the structure of the lymphatic glands, that they must materially retard the passage of the lymph toward the great trunks; and it is well known in pathology that morbid matters taken up by the absorbents are frequently arrested and retained in the nearest glands.

The function of the lymphatic glands is very obscure. By some they are supposed to have an important office in the elaboration of the corpuscular elements of the lymph and chyle; and it has been observed that the lymph contained in vessels which have passed through no glands is relatively poor in corpuscles, while the large trunks and the efferent vessels contain them in large numbers. This single fact is indefinite enough, as regards the mode of formation of the lymph-corpuscles, but it represents about all that is actually known concerning the function of the lymphatic glands.

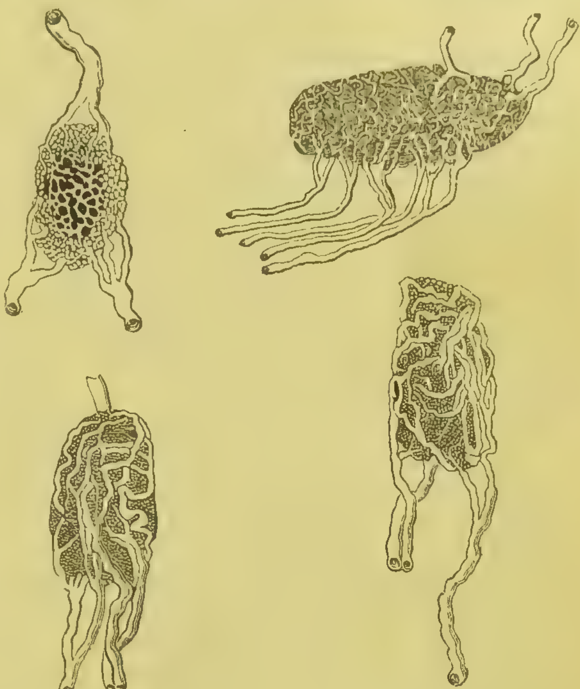


FIG. 93.—*Different varieties of lymphatic glands.* (Sappey.)

In endeavoring to estimate the share which the lacteals and lymphatics have in the function of absorption, it becomes an important question to determine what principles these vessels are capable of taking up, beside the fatty elements of the food, and how far, if at all, they assist the blood-vessels in the absorption of the general products of digestion.

Absorption of Albuminoids by the Lacteals.—Comparative analyses of the lymph and chyle always show in the latter fluid an excess of albuminoid matters. As we may reasonably suppose that, during the intervals of digestion, the lacteals carry ordinary lymph—for, at this time, these vessels are filled with a colorless, transparent fluid, having the general physical characters of lymph—it is natural to infer that the excess of nitrogenized matters in the white chyle is due to absorption of albuminoids from the intestinal canal. Mr. Lane collected the chyle from the lacteals of a donkey, seven and a half hours after a full meal of oats and beans, and compared its composition with that of the lymph. The analyses were made by Dr. Rees, who found that the chyle contained about three times as much albumen and fibrin as the lymph. While by far the greater part of the products of digestion of the albuminoids is absorbed by the blood-vessels, there can be no doubt that a small portion is also taken up by the lacteals.

Absorption of Glucose and Salts by the Lacteals.—What has just been stated regarding the absorption of albuminoids applies with equal force to saccharine matters and the inorganic salts. Small quantities of sugar and sometimes lactic acid have been detected in the chyle from the thoracic duct in the herbivora; and the presence of sugar in both the lymph and the chyle has been accurately determined by Colin.

It is true that the products of the digestion of saccharine and amylaceous matters are taken up mainly by the blood-vessels, but a small quantity is also absorbed by the lacteals. In the comparative analyses of the chyle and lymph by Dr. Rees, the proportion of inorganic salts was found to be considerably greater in the chyle. The great excess in the quantity of blood coming from the intestine and the rapidity of its circulation, as compared with the chyle, will explain the more rapid penetration by endosmosis of the soluble products of digestion.

Absorption of Water by the Lacteals.—There can be no doubt that a small portion of the liquids taken as drink finds its way into the circulation by the lacteals, although the greatest part passes directly into the blood-vessels. This has been proven by experiments of a most positive character. Leuret and Lassaigne state that, when an animal is fed with an aliment which is very substantial and is killed during digestion, the thoracic duct contains a very small quantity of chyle; but, when the animal has taken liquids with the food, the thoracic duct and the lacteals are very much distended. In an experiment by Ernest Burdach, a dog was deprived of food and drink for twenty-four hours, after which he was allowed to drink water, and, in addition, half a pound was injected into the stomach. The animal was killed a half an hour after, and the thoracic duct was found engorged with watery lymph, which contained a very small number of lymph-corpuscles.

In discussing the question of absorption by the blood-vessels of the intestinal canal, we alluded to experiments which showed that various poisonous substances introduced into the intestines produced their characteristic effects upon the system with great rapidity when the veins leading from the part were intact, while no such effects followed when the only avenue to the general system was through the lacteals. Without again discussing these observations in detail, it may be stated, as the general results of experiments on this subject, that few, if any, of the active poisons were found to be absorbed from the alimentary canal, except by blood-vessels; and, when soluble coloring matters, or salts which could be easily recognized, were found in the lacteals or the thoracic duct after they had been introduced into the intestine, they penetrated in small quantity and very slowly; while it has been repeatedly found that the same substances were taken up by the veins with great rapidity and excreted, in many instances, by the urine.

Absorption from Parts not connected with the Digestive System.—Aside from the entrance of gases into the blood from the pulmonary surface, physiological absorption is almost entirely confined to the mucous membrane of the alimentary canal. It is true that liquids may find their way into the circulation through the skin, the lining membrane of the air-passages, the reservoirs, ducts, and parenchyma of glands, the serous and other closed cavities, the areolar tissue, the conjunctiva, the muscular tissue, and, in fact, all parts which are supplied with blood-vessels; but here the absorption of foreign matters is an occasional or an accidental circumstance and is not connected with the general process of nutrition. It is now well known that all parts of the body, except the epidermis and its appendages, the epithelium, and some other structures which are regularly desquamated, are constantly undergoing change, and the effete matters which result from their decay are taken up by what is called interstitial absorption and are carried by the blood to the proper organs, to be excreted. It seems probable that the vessels of these parts would also be capable of taking up soluble foreign substances when presented to them; and this is, indeed, the fact with regard to all parts in which the nutritive processes are even moderately active, or where the structures covering the vascular parts are permeable.

Absorption from the Skin.—It is now generally admitted that absorption can take place from the general surface, although, at one time, this was a question much discussed by physiologists and practical physicians. The proofs, however, of the entrance of certain medicinal preparations from the surface of the body are now entirely conclusive; and the constitutional effects of medicines administered in this way are frequently as marked as when they are taken into the alimentary canal. But the question which is of most interest to us as physiologists concerns the normal functions of the skin as an absorbing surface. Looking at this subject from a purely physiological point of view, absorption from the skin, under ordinary conditions, must be very slight, if, indeed, it take place at all. There are a few observations by the older physiologists which would at first seem to show that a certain amount of water is taken up by the skin when the atmosphere is unusually moist. In all of these, however, this conclusion is drawn from the circumstance that the weight is occasionally somewhat increased under these conditions; but no account is taken of the fact, that, when the surrounding atmosphere is moist, the amount of the exhalations is greatly decreased. The lungs, also, present an immense absorbing surface, which is not at all considered. Experiments on this point are not sufficiently definite to warrant any positive conclusions; but it is evident that, if any articles enter in this way, the quantity must be excessively minute.

The experiments upon the entrance of water and soluble substances through the skin, when the body has been immersed for a long time in a bath, are somewhat contradictory. Most experimenters have noted an increase in the weight, which they attribute to absorption of water, but others profess to have observed a slight diminution in the weight of the body. In some experiments on this subject, by Madden, in which all necessary precautions were adopted, the air being respired through a tube passed out of the window of the room, so that no unusual absorption of moisture could take place by the lungs, the results were very conclusive. In experiments of this kind, there are many modifying influences to be guarded against. For example, it has been found to be important to regulate carefully the temperature of the bath; for, when it exceeds that of the body, there may be a loss of weight by cutaneous transpiration. It is stated by Longet that, when the temperature of the water is lower than that of the body, there is a gain in weight; but that the cutaneous exhalation and absorption are balanced when the temperature of the bath and the body are the same. There is another source of complication in these observations, which has been brought forward very strongly by a French writer, M. Delore. This observer has carefully noted the increase in weight of the hair, nails, and epidermis, after immersion for half an hour in distilled water, and has always found it to be very considerable. He assumes that this is more than sufficient to account for the increase in the weight of the entire body after immersion in water for half an hour, which amounts to about seven hundred grains.

There are, nevertheless, facts which render it certain that water can be absorbed by the skin. In an elaborate series of experiments by Collard de Martigny, it was proven conclusively that water could be absorbed in small quantity by the skin of the palm of the hand. In one experiment, a small bell-glass filled with water was applied hermetically to the palm. This was connected with a tube bent in the form of a siphon, also filled with water, the long branch of which was placed in a vessel of mercury. After the apparatus had been applied for an hour and three-quarters, the mercury was found sensibly elevated in the tube, showing that a certain quantity of the water had disappeared. More recently, a very extended series of observations upon the absorption of water and soluble substances has been made by Dr. Willemin, in which it is conclusively proven that water is absorbed in a bath, and that various medicinal substances may be taken up by the skin in this way and can be detected afterward in the urine. In a large number of experiments, he found that the weight of the body, after remaining in a tepid bath for from thirty to forty-five minutes, was generally stationary; but that sometimes there was a very slight diminution in weight and sometimes a very slight increase. By comparative observations, however, he found that the diminution of weight in the bath was always less than the amount lost by the same subject in the air. Dr. Willemin employed a very delicate apparatus for weighing, and his observations were apparently conducted with great care. He also confirmed the statement of W. F. Edwards and others, that transpiration from the general surface goes on in a bath. This he showed by differences in the composition of the bath before and after immersion of the body.

These observations do much to reconcile the contradictory experiments of others, in some of which a diminution in weight was observed, while in some an increase was noted. In studying this subject, it must always be remembered that there is a constant loss of weight by evaporation from the general surface and from the lungs; a fact which was not taken into account by some of the earlier experimenters.

It has been frequently remarked that the sensation of thirst is always least pressing in a moist atmosphere, and that it may be appeased to a certain extent by baths. It is true that, in a moist atmosphere, the cutaneous exhalations are diminished, and this might account for the maintenance of the normal proportion of fluids in the body with a less amount of drink than ordinary; but we could hardly account for an actual allevia-tion of thirst by immersion of the body in water, unless we assumed that a certain quantity of water had been absorbed. A striking example of relief of thirst in this way is given by Captain Kennedy, in the narrative of his sufferings after shipwreck, when he and his men were exposed for a long time without water, in an open boat. With regard to his sufferings from thirst, he says: "I cannot conclude without making mention of the great advantage I derived from soaking my clothes twice a day in salt-water, and putting them on without wringing. . . . There is one very remarkable circum-stance, and worthy of notice, which was, that we daily made the same quantity of urine as if we had drunk moderately of any liquid, which must be owing to a body of water absorbed through the pores of the skin. . . . So very great advantage did we derive from this practice, that the violent drought went off, the parched tongue was cured in a few minutes after bathing and washing our clothes; at the same time we found ourselves as much refreshed as if we had received some actual nourishment."

Absorption by the Respiratory Surface.—In studying the physiological anatomy of the respiratory apparatus, we have seen how admirably the respiratory surface is calcu-lated for the introduction of gaseous principles into the blood. The great rapidity with which the oxygen of the inspired air penetrates through the delicate covering of the pul-monary vessels has already been fully considered under the head of respiration. Under natural conditions, the gases of the air are the only principles absorbed by the lungs; but examples of the absorption of other gaseous matters are exceedingly common, and this process has been the subject of numerous experiments by physiologists. The fact of the absorption of foreign substances by the lungs, also, has long been definitely settled; but this belongs to pathology or to therapeutics, rather than to physiology.

It is now almost universally conceded that animal and vegetable emanations may be taken into the blood by the lungs and produce certain well-marked pathological condi-tions. It is supposed that many contagious diseases are propagated in this way, as well as some fevers and other general diseases which are not contagious. With regard to cer-tain poisonous gases and volatile principles, the effects of their absorption by the lungs are even more striking. Carbonic oxide and arseniuretted hydrogen produce death al-most instantly, even when inhaled in small quantity. The vapor of pure hydrocyanic acid acts frequently with great promptness through the lungs. Turpentine, iodine, and many medicinal substances may be introduced with great rapidity by inhalation of their va-pors; and we well know the serious effects produced by the emanations from lead or mer-cury in persons who work in these articles. Among the most striking proofs of the absorption of vapors by the lungs are the effects of the inhalation of ether. This passes into the blood and manifests its characteristic anæsthetic influence almost immediately. Not only have vapors introduced in this way been recognized in the blood, but many of the principles thus absorbed are excreted by the kidneys and may be recognized by their characteristic reactions in the urine.

As would naturally be expected, water and substances in solution, when injected into the respiratory passages, are rapidly absorbed, and poisons administered in this way manifest their peculiar effects with great promptness. Experimenters on this subject have shown the facility with which liquids may be absorbed from the lungs and the air-passages, but it must be remembered that the natural conditions are never such as to admit of this action. The normal function of the lungs is to absorb oxygen and sometimes a little nitrogen from the air; and the absorption of any thing else by these surfaces is unnatural and generally deleterious.

Absorption from Closed Cavities, Reservoirs of Glands, etc.—Facts in pathology showing absorption from closed cavities, the areolar tissue, the muscular and nervous tissue, the conjunctiva, and other parts, are sufficiently numerous. In all cases of effusion of serum into the pleural, peritoneal, pericardial, or synovial cavities, in which recovery takes place, the liquid becomes absorbed. It has been shown by experiment that warm water injected into these cavities is disposed of in the same way. Effusions into the areolar tissue are generally removed by absorption. In cases of penetration of air into the pleura or the general areolar tissue, absorption likewise takes place; showing that gases may be taken up in this way as well as liquids. Effusions of blood beneath the skin or the conjunctiva or in the muscular or nervous tissue may become entirely or in part absorbed. It is true that these are pathological conditions, but, in the closed cavities, the processes of exhalation and absorption are constantly going on, although not very actively. As regards absorption from the areolar tissue, the administration of remedies by the hypodermic method, which is now so common, is a familiar proof of the facility with which soluble principles are taken into the blood when introduced beneath the skin.

Under some circumstances, absorption takes place from the reservoirs of the various glands, the watery portions of the secretions being generally taken up, leaving the solid and the organic matters. It is supposed that the bile becomes somewhat inspissated when it has remained for a time in the gall-bladder, even when the natural flow of the secretion is not interrupted. Certainly, when the duct is in any way obstructed, absorption of a portion of the bile takes place, as is proven by coloration of the conjunctiva and even of the general surface. The serum of the blood, under these conditions, is always strongly colored with bile.

It is probable that some of the watery portions of the urine are reabsorbed by the mucous membrane of the urinary bladder, when the urine has been long confined in its cavity, although this resorption is ordinarily very slight. A great many cases of discharge of urinary matters by the stomach and intestines, skin, etc., when the urine has been long retained, have been reported by the older physiologists and were supposed to indicate resorption of these principles from the bladder. The mechanism of the excretion of urinary matters was not understood before the experiments of Prévost and Dumas, who showed that urea accumulates in the blood after the extirpation of both kidneys in the inferior animals. It is now generally admitted that this takes place when the function of excretion of urine is seriously interfered with, and that an attempt is made by Nature to remove these effete principles from the system by the stomach, intestine, skin, and lungs. It is possible, therefore, that the vicarious discharge of urinary matters, in the cases reported before the true process of excretion by the kidneys was understood, was due to accumulation of the constituents of the urine in the blood, and not to their resorption from the urinary passages.

Absorption may take place from the ducts and the parenchyma of glands, although this occurs chiefly when foreign substances have been injected into these parts.

Absorption of Fats and Insoluble Substances.

The general proposition that all substances capable of being absorbed are soluble in water or in the digestive fluids must be modified in the case of the fats. These are never dissolved in any appreciable quantity in digestion, the only change which they undergo being a minute subdivision in the form of a very fine emulsion. In this condition, the fats are taken up by the lacteals and may be absorbed in small quantity by the blood-vessels. Although it is now pretty well understood how endosmotic liquids pass through the walls of the blood-vessels and absorbents, the mechanism of the penetration of fatty particles, which is no less constant, is still somewhat obscure.

There can be no question with regard to the actual penetration of the minute particles of the chyle into the lacteals and even into the blood-vessels. In birds, indeed, according to Bernard, all the fat which is absorbed is taken up by the blood-vessels, the lymphatics of the intestine never containing a milky fluid. Confining our discussion to the mechanism of the absorption of fatty emulsion in mammals, it must be admitted that the assumption of the existence of orifices in the walls of the lacteals, even if we deny the actual anatomical demonstration of these openings, becomes almost necessary; for the experiments upon the passage of fatty particles through closed membranes are certainly very unsatisfactory. Taking into consideration all of the facts bearing upon the question, it seems more probable that orifices exist in the vessels than that the fatty particles penetrate by endosmosis; but it must be remembered that this idea rests upon the undoubted physiological fact of the absorption of emulsions rather than upon anatomical grounds; and, if we were not called upon to explain the absorption of fatty particles, it is doubtful whether the stomata of the vessels would be so generally admitted. It is not infrequently the case that we are forced to assume the existence of certain anatomical arrangements as the only reasonable explanation of physiological phenomena, when actual demonstrations are unsatisfactory. With regard to the lacteals, when we remember the excessive tenuity of the vessels of origin, the close adhesion of their walls to the surrounding tissues, the novelty and uncertainty of the staining processes, and the fact that some anatomists deny that the finest so-called lymphatic plexuses of origin have any distinct walls, it is readily understood how, as physiologists, we must regard the existence of stomata in the lymphatics as an idea based upon the necessity of explaining well-established physiological phenomena, rather than a clearly-demonstrable anatomical fact.

In studying the mechanism of the penetration of fatty particles into the intestinal villi, it has been ascertained that the epithelial cells covering the villi play an important part in this process. It was first ascertained by Goodsir that, during the digestion of fat, these cells became filled with fatty granules. This fact has been confirmed by Gruby and Delafond, Kölliker, Funke, and others. Funke, in his atlas of physiological chemistry, figures the appearances of the intestinal epithelium during the digestion of fat, as contrasted with the epithelium observed during the intervals of digestion, showing the cells, during absorption, filled with fatty granules.

FIG. 94.—*Epithelium of the small intestine of the rabbit.* (Funke.)

It is true, as a general law, that insoluble substances, with the exception of the fats, are never regularly absorbed, no matter how finely they may be divided. The apparent exceptions to this are, mercury in a state of minute subdivision like an emulsion, and carbonaceous particles. In the case of mercury, it is well known that minute particles in the form of unguents may be introduced into the system by prolonged frictions; but this cannot be regarded as an instance of physiological absorption. The passage of small carbonaceous particles through the pulmonary membrane seems to be purely mechanical. The same thing may possibly occur when fine, sharp particles of carbon are introduced into the alimentary canal; but the experiments of Mialhe with pulverized charcoal, and particularly those of Bérard, Robin, and Bernard with lamp-black introduced into the intestinal canal of animals, showed that, although the intestinal mucous membrane became of a deep black, this could easily be removed by a stream of water, and no carbonaceous particles could be discovered in the mesenteric veins, the lacteals, or the mesenteric glands. When the carbon is used in the form of lamp-black, the particles are very minute and rounded, and they do not present the sharp points and edges which sometimes enable the grains of pulverized charcoal to penetrate the vessels mechanically.

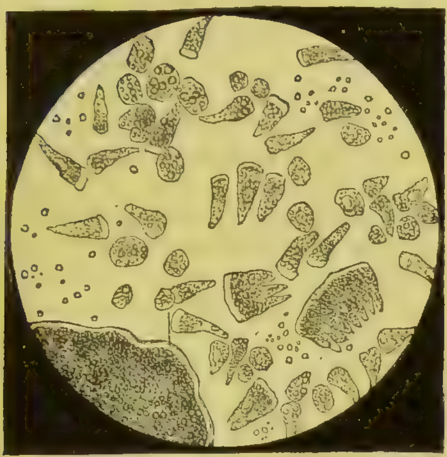


FIG. 95.—*Epithelium from the duodenum of a rabbit, two hours after having been fed with melted butter.* (Funke.)

FIG. 96.—*Villi, filled with fat, from the small intestine of an executed criminal, one hour after death.* (Funke.)

Variations and Modifications of Absorption.

Very little is known concerning the variations in lacteal or lymphatic absorption; but, in absorption by blood-vessels, important modifications occur, due, on the one hand, to different conditions of the fluids to be absorbed, and, on the other, to differences in the constitution of the blood and in the conditions of the vessels.

The different conditions of the fluids to be absorbed apparently do not always have the same influence in physiological absorption as in endosmotic experiments made out of the body. Saccharine solutions of different densities confined in distinct portions of the intestinal canal of a living animal do not present any marked variations in the rapidity of their absorption, and they are taken up by the blood, even when their density is greater than that of the blood-plasma. Solutions of nitrate of potash and sulphate of soda of greater density than the serum, which would, therefore, attract the endosmotic current in an endosmometer, are readily taken up by the blood-vessels in a living animal. Indeed, nearly all soluble substances, whatever be the density of their solutions, may be taken up by the various absorbing surfaces during life. The woorara poison and most of the venoms are remarkable exceptions to this rule. In a series of very interesting experiments upon the absorption of woorara, Bernard has shown that this curious poison, which is absorbed so readily from wounds or when introduced under the skin, generally produces no effect when introduced into the stomach, the small intestine, or the urinary bladder. This result, however, is not invariable, for poisonous effects are produced when woorara is introduced into the stomach of a fasting animal. This peculiarity in the absorption of many of the animal poisons has long been observed; and it is well known that the flesh of animals poisoned with woorara can be eaten with impunity. It is curious, however, to see an animal carrying in the stomach without danger a fluid which would produce death if introduced under the skin; and the explanation of this is not readily apparent. The poison is not neutralized by the digestive fluids, for woorara digested for a long time in gastric juice, or taken from the stomach of a dog, is found to possess all its toxic properties, as we have frequently shown (repeating the experiment of Bernard) by poisoning a pigeon with woorara drawn by a fistula from the stomach of a living dog. If we recognize the absorption of this poison simply by its effects upon the system, it must be assumed that, during digestion, it cannot be absorbed by the mucous membrane of the stomach and small intestine, notwithstanding that it is exceedingly soluble.

It has also been shown that liquids which immediately disorganize the tissues, such as concentrated nitric or sulphuric acid, cannot be absorbed. Another important peculiarity in absorption has been demonstrated by Mialhe, who has shown that solutions which readily coagulate the albumen of the circulating fluids are absorbed very slowly. This is explained on the supposition that there is a coagulation of the albuminous fluids with which the absorbing membrane is permeated, which interferes with the passage of liquids. These substances are nevertheless taken up by the blood-vessels, though rather slowly.

The modifications which are due simply to the physical conditions of liquids to be absorbed are chiefly manifested out of the body and will be considered in connection with the subject of endosmosis.

Influence of the Condition of the Blood and of the Vessels on Absorption.—After loss of blood or deterioration of the nutritive fluid from prolonged abstinence, absorption generally takes place with great activity. This is well known, both as regards the entrance of water and alimentary substances and the absorption of medicines. It was at one time quite a common practice to bleed before administering certain remedies, in order to produce their more speedy action upon the system.

The rapidity of the circulation has an important influence upon absorption. We have already shown, in treating of the action of the blood-vessels on absorption, that this process may be impeded or even arrested by the ligation of important vessels. It has been evident, also, that absorption is generally active in proportion to the vascularity of different parts. During the process of intestinal absorption, the increase in the activity of the circulation in the mucous membrane is very marked and undoubtedly has an influence upon the rapidity with which the products of digestion are taken up.

Influence of the Nervous System on Absorption.—Experiments upon the influence of the nervous system on absorption are still very imperfect. It is certain that this process, especially in the stomach, is subject to variations, which can hardly be dependent upon any thing but nervous action. Water and other liquids, which usually are readily absorbed from the stomach, are sometimes retained for a time, and are afterward rejected in nearly the condition in which they were taken. It is probable, however, that the most important influences thus exerted by the nervous system are effected through the circulation. The recent experiments of Bernard and others upon the sympathetic system of nerves and its connection with the muscular coats of the small arteries, by the action of which the supply of blood in different parts is regulated, point out a line of experimentation which would probably throw much light upon some of the important variations in absorption. When it is remembered that the small arteries may become so contracted under the influence of the sympathetic system that their caliber is almost obliterated, of course retarding to a corresponding degree the capillary and venous circulation in the parts, and, again, that, through the sympathetic nerves, the same vessels may be so dilated as to admit to a particular part three or four times as much blood as it ordinarily receives, it becomes apparent that absorption may be profoundly affected through this system of nerves.

As far as the influence of the cerebro-spinal system is concerned, it has been ascertained that, while section of some of the nerves distributed to the alimentary canal will slightly retard the absorption of poisonous substances, it is never entirely arrested. Longet found that the operation of strychnine injected into the stomach of a dog in which both pneumogastric nerves had been divided was retarded about five minutes; but that the convulsions, when they occurred, were fully as severe as in an animal which had received an equal dose, without section of the nerves.

Imbibition and Endosmosis.

The ideas of physiologists concerning the mechanism of the absorption of soluble substances have become radically changed since the beginning of the present century; and it is now generally admitted that this process takes place chiefly by blood-vessels, and that the absorbents have no such wonderful elective power as was attributed to them by the older writers. This involves the passage of liquids through the coats of the blood-vessels and lymphatics; a process which has been the subject of numerous experiments, resulting in the development of many important physical laws capable of application to physiological absorption. At the present day, therefore, the history of absorption is not complete without a consideration of the laws of imbibition and endosmosis.

If liquids can pass through the substance of an animal membrane, it is evident that the membrane itself must be capable of taking up a certain portion of the liquid by imbibition; and this must be considered as the starting-point in absorption. Imbibition is, indeed, a property common to all animal structures. One of the most striking characteristics of organic principles is that they may lose water by desiccation and regain it by imbibition. It is also a well-known fact that the tissues do not imbibe all solutions with the same degree of activity. Distilled water is the liquid which is always taken up in greatest quantity, and saline solutions enter the substance of the tissues in an inverse ratio to their density. This is also the fact with regard to mixtures of alcohol and water, imbibition always being in an inverse proportion to the quantity of alcohol present in the liquid. Among the other circumstances which have a marked influence upon imbibition, is temperature. It is a familiar fact that dried animal membranes may be more rapidly softened in warm than in cold water; and, with regard to the imbibition of liquids by sand, the researches of Matteucci and Cima have shown an immense increase at a moderately-elevated temperature. While nearly all the structures of the body, after desiccation, will imbibe liquids, the membranes through which the processes of absorption are most active are, as a rule, most easily permeated; and we shall see, when we come to study the mechanism of the passage of liquids through these membranes, that the character of the liquid, the temperature, etc., have a great influence upon the activity of this process. For example, all liquids which have a tendency to harden the tissues, such as saline solutions, alcohol, etc., pass through with much less rapidity than pure water. These facts will be found particularly interesting in connection with observations on the passage of liquids through membranes, in experiments on endosmosis with artificial apparatus.

Mechanism of the Passage of Liquids through Membranes.—The attention of physiologists was first directed to this subject by the researches of Dutrochet, in 1826. Although not by any means the first to observe the phenomena which he described under the name of endosmosis, to Dutrochet is generally ascribed the honor of having first indicated the applications of the laws of endosmosis to the nutrition of plants and animals. Undoubtedly, Dutrochet was the first to make experiments upon endosmosis which attracted the attention of scientific men in different parts of the world and which were immediately repeated and extended; but the experiments made upon living animals by Lebküchner, in 1819, and by Magendie, in 1820, had already demonstrated most conclusively the passage of liquids through the walls of the blood-vessels; and the explanation offered by these physiologists was fully as definite as that proposed by Dutrochet.

Dutrochet constructed an instrument called the endosmometer, which consists simply of a small bell-glass, the lower opening of which is closed by a membrane, the opening above being connected with a long glass tube by which the force with which liquids pass through the membrane can be measured. The bell-glass is generally filled with a liquid capable of attracting a current of water from without, and is immersed in pure water, so that the membrane is completely covered. Under these circumstances, there is a current of water through the membrane, which will cause the liquid to mount in the tube, sometimes to the height of several feet; but, at the same time, there is a feebler current from the interior of the apparatus to the water. Dutrochet called the stronger, the endosmotic current, and the feebler, the exosmotic current. This nomenclature, however, is not strictly accurate; for, if the position of the liquids be reversed, the stronger current is exosmotic and the feebler is endosmotic. It must be remembered, therefore, that the name endosmosis is always to be understood as applied to the principal current, while the term exosmosis is applied to the current in the opposite direction. This possible inaccuracy of expression has led to the adoption by Graham and others of the term osmosis, as applied generally to the currents which take place through membranes; but the terms first proposed by Dutrochet are most commonly used.

The phenomena of endosmosis, which, since the publication of the researches of Dutrochet, have been so closely studied by physicists, are chiefly interesting to the physiologist in their application to absorption. While it is true, perhaps, that all the phenomena of physiological absorption cannot as yet be explained upon purely physical principles, it is nevertheless important to ascertain how far physical laws are involved in this process. With this end in view, we shall study the physical phenomena of endosmosis, chiefly with reference to their physiological applications.

It is now definitely ascertained that the following conditions are necessary for the operation of endosmosis and exosmosis:

1. That both liquids be capable of "wetting" the interposed membrane, or, in other words, that the membrane be capable of imbibing both liquids. If but one of the liquids can wet the membrane, the current can take place in only one direction.

2. That the liquids be miscible with each other and be differently constituted. Although it is found that the currents are most active when the liquids are of different densities, this condition is not indispensable; for currents will take place between solutions of different substances, such as salt, sugar, or albumen, when they have precisely the same density.

The physiological applications of the laws of endosmosis can now be more fully appreciated, as it is evident that the above conditions are fulfilled whenever absorption takes place, with the single exception of the absorption of fats, which has been specially considered. For example, all substances are dissolved or liquefied before they are absorbed, and, in this condition, they are capable of "wetting" the walls of the blood-vessels. All the liquids absorbed are capable, also, of mixing with the plasma of the blood. What makes this application still more complete, is the behavior of albumen in endosmotic experiments. In physiological absorption, there is always a great predominance of the endosmotic current, and there is very little transudation, or exosmosis, of the albuminoid constituents of the blood. On the other hand, there is a constant absorption of albuminose, which is destined to be converted into the albuminoid matters of the blood.

Recognizing the fact, which was, indeed, pointed out clearly by Dutrochet, that albumen is capable of inducing a more powerful endosmotic current than almost any other liquid, it has been shown that it never itself passes through membranes in the exosmotic current; but that albuminoids, after transformation by digestion into albuminose, or albumen mixed with gastric juice, pass through animal membranes with great facility. The experiments by which these facts are demonstrated are very conclusive and are of the highest physiological importance. On removing part of the shell of an egg, so as to expose its membranes, and immersing it in pure water, the passage of water into the egg was rendered evident by the projection of the distended membranes; but, although the surrounding liquid had become alkaline and the appropriate tests revealed the presence of some of the inorganic constituents of the egg, the presence of albumen could never be detected. When the contents of the egg were replaced by the serum of the blood, the same result followed. "After six or eight hours of immersion, the serum had yielded to the water in the vessel all its saline elements, chlorides, sulphates, phosphates, which were easily recognized by their peculiar reactions, but not an atom of albumen."

A very simple apparatus for illustrating endosmotic action can be constructed in the following way: Remove carefully a circular portion, about an inch in diameter, of the shell from one end of an egg, which may be done without injuring the membranes, by cracking the shell into small pieces, which are picked off with forceps. A delicate glass-tube, about six inches in length, is then introduced through a small opening in the shell and membranes of the other end of the egg, and is secured in a vertical position by wax, the tube penetrating the yolk. The egg is then placed in a wine-glass partly filled with water. In the course of half an hour or an hour, the water will have penetrated the exposed membrane, and the yolk will rise in the tube.

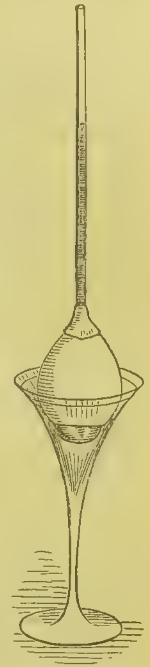


FIG. 97.—*Egg prepared so as to illustrate endosmotic action.*

Influence of Membranes upon Osmotic Currents.—The force with which liquids pass through membranes, called endosmotic or osmotic force, is to a great degree dependent upon the influence of the membranes themselves. This influence is always purely physical, in experiments made out of the body; and physiological absorption can be explained, to a certain extent, by the same laws. It must be remembered, however, that the properties of organic structures, which are manifested only in living bodies, are capable of modifying these physical phenomena to a remarkable degree. For example, all living tissues are capable of selecting and appropriating from the nutritive fluids the materials necessary for their regeneration; and the secreting structures of glands also select from the blood certain principles which are used in the formation of their secretions. At the present day, these phenomena and their modifications through the nervous system cannot be fully explained. This is true, also, of many of the phenomena of absorption and their modifications, which are probably dependent upon the same kind of action. In view of these undoubted facts, the influence of the structures through which liquids pass in physiological absorption may be divided as follows: first, into physical influences, which may be illustrated by endosmotic experiments with organic membranes out of the body; and second, modifications of these phenomena, which are presented only in the living organism.

Numerous experiments have demonstrated that both the endosmotic and the exosmotic current may be produced by using a porous instead of a membranous septum, though then they are always comparatively feeble. The phenomena thus presented are to be explained entirely by the laws of capillary attraction and of the diffusion of liquids. These laws would enter largely into the explanation of the passage of liquids through animal membranes, if it could be demonstrated, or even rendered probable, that these membranes are invariably porous, or provided with capillary openings. It will be necessary, however, to study this question very carefully and to examine all the properties of animal membranes, both within and without the living organism.

In the first place, is there any proof that all membranes which will admit the passage of liquids are porous? This is a most important question; and it lies at the foundation of the explanation of the phenomena of endosmosis by the laws of capillary attraction.

In all membranes which possess an anatomical structure discoverable by the microscope, there are undoubtedly interstices between the fibres, cells, etc., of which the tissue is composed; but, on the other hand, animal membranes generally have a layer, like the basement-membranes of mucous tissues, which is absolutely homogeneous and structureless. In applying the laws of endosmosis to physiological absorption, it is found that the membranes which are most easily penetrated by fluids are excessively thin and nearly homogeneous. Take, for example, the walls of the capillary blood-vessels, through which the greatest part of physiological absorption takes place. This membrane is from $\frac{1}{25000}$ to $\frac{1}{12500}$ of an inch thick, and is entirely amorphous, with the exception of the lining epithelium with its nuclei. The assumption that invisible capillary orifices exist in these thin, amorphous membranes, aside from the so-called stomata, is purely hypothetical and is unwarrantable. The only circumstance which could lead to such a supposition is the fact that these membranes can be penetrated by liquids.

It is manifestly unphilosophical and absurd to offer, as an explanation of endosmosis through structureless membranes, an hypothesis which has its only support in the existence of the phenomena which it is intended to explain. This mode of reasoning is all the more unsound, as the phenomena of endosmosis are very far from being completely understood, and as many important properties of organic structures, which bear directly upon the question under consideration, are ignored. For example, physiological absorption does not always take place in accordance with known physical laws. It undergoes modifications which can at present only be explained on the supposition that the liquids become, for the time, part of the living organic structures and partake of their peculiar properties; one of them, the property by virtue of which they appropriate both the organic and the inorganic principles necessary to their proper constitution and regeneration, is called by some, vital; a word which simply expresses ignorance of its essential character. It must be understood, however, that this remark does not apply to the general phenomena of endosmosis or absorption, but only to certain of its unexplained modifications.

A most important property of organic tissues, which is ignored by those who explain absorption on the principle of capillary attraction, is that of hygrometricity. All the organic nitrogenized proximate principles are capable of losing their water of composition by desiccation and of regaining it by imbibition. The water which enters into their composition is not necessarily contained in interstices in the tissue, but, in the case of structureless parts especially, is uniformly disseminated, or, we may term it, diffused throughout the organic substance, of which it forms a constituent part. This action of certain liquids upon the organic semisolids is something like the diffusion of liquids; the difference being that it is the liquid only which is diffused in the semisolid, the semisolid being incapable of diffusing in the liquid. As it has been found that all liquids are not equally subject to capillary attraction, so animal tissues imbibe different liquids with different degrees of activity; a fact which will account in a measure for the variations in the endosmotic currents with different solutions.

Examples are not wanting of endosmosis by imbibition or diffusion, when it cannot be assumed that there is any such thing as porosity in the septum. The following experiment of Lhermite fully illustrates this point. A tube was partly filled with a column of chloroform; and upon this was poured a layer of water, and above it a layer of ether. The ether gradually penetrated the layer of water and passed to the chloroform, mingling with it. After a certain time, all the ether had thus been diffused in the chloroform, and the layer of water retained its original volume. We have repeated this experiment with some slight modifications, using first a layer of sulphuric acid, then a layer of water, and finally a solution of blue litmus in alcohol; and, in a very short time, the acid penetrated the water and reddened the litmus above. A liquid septum is certainly not porous, in any sense of the word; and the explanation of the phenomenon of endosmosis through liquids depends simply upon the law of diffusion of liquids, the molecules of the liquids being held together so feebly that they will admit the molecules of other liquids with which they are capable of mixing.

With regard to the passage of liquids through different septa, the following seem to be the facts which can be considered as definitely settled:

The cohesive attraction of the constituent particles of insoluble solids is so great, that the entrance of fluids is impossible, unless the substance be porous, and this always involves the law of capillary attraction; but, in liquids, the cohesive attraction is so slight as to admit of the penetration and diffusion of certain other liquids.

Homogeneous animal membranes, which are of a semisolid consistence, are capable of imbibing certain liquids; and any liquid which can pass into such membranes will pass through them under proper conditions. The cohesive attraction of the particles of the membrane is not such as to allow them to imbibe an indefinite quantity of any liquid; but it is one of the distinctive properties of organic tissues, that a limited quantity of liquid can be taken up in this way.

In view of these facts, it is not necessary to assume the existence of infinitely small capillary openings in homogeneous membranes through which osmotic currents can be made to take place, in order to explain the mechanism of these currents. In the case of two liquids capable of diffusing with each other and separated by an animal membrane, the mechanism of the endosmotic and exosmotic currents is very simple. In the first place, the membrane imbibes both the liquids, but one is always taken up in greater quantity than the other. If water and a solution of common salt be employed, the surface of the membrane exposed to the water will imbibe more than the surface exposed to the saline solution; but both liquids will meet in its substance. The first step, therefore, in the production of the currents is imbibition. Once in contact with each other, the liquids diffuse, the water passing to the saline solution, and *vice versa.* This takes place by precisely the same mechanism as that of the passage of liquids through porous septa.

The osmotic currents may be modified with the same liquids by using different membranes. This fact was well illustrated in some of the experiments of Matteucci and Cima, in which comparative observations were made upon the currents through the skin of the torpedo, the skin of the frog, and the skin of the eel. The results obtained with these different membranes showed marked and constant variations. The same observers, using the mucous membrane of the stomach of the lamb, found a marked difference in the endosmotic phenomena when the surface exposed to the water was reversed. In two experiments, with the epithelial surface of the membrane turned toward the interior of the endosmometer, the elevations of the liquid in an hour and a quarter were forty-four and fifty-six millimeters; but, with the membrane reversed, so that the attached surface was turned toward the interior, the elevations during the same period were sixty-six and seventy-two millimeters. This difference is readily explained by the difference in the constitution of the two surfaces of the membrane used. From these facts, it is evident that, while the diffusion of liquids as they meet in the substance of a membrane is the actual cause of the osmotic currents, which are continued as the liquids diffuse with each other upon either side of the membrane, the determination of a predominating or endosmotic current, the ordinary conditions being undisturbed, is effected by the greater attractive force which the membrane exerts upon one of the liquids.

Influence of Different Liquids upon Osmotic Currents.—The action of the liquids between which endosmotic currents take place is, as we have seen, most intimately connected with the force by which the liquids enter the membrane, be it capillary attraction or imbibition; but the attractive force exerted by the membrane is never capable, in itself, of producing a current. It is evident, therefore, that the properties of the liquids must have an important influence upon osmosis, both from differences in the attraction of the membrane for the liquids and their different degrees of diffusibility. In order to appreciate fully all the physical phenomena of osmosis, it will be necessary to study carefully the laws of diffusion of liquids and the diffusibility of different solutions; but it will be sufficient for our present purpose to state a few general propositions, which will be found more or less applicable to physiological absorption.

When two liquids, capable of mixing with each other, are brought together, they diffuse with greater or less rapidity, until the constitution of the mixture becomes uniform.

Different liquids possess widely different degrees of diffusibility; and, as a rule, in saline solutions, the rate of diffusion increases in proportion to the strength of the solution, at least when the quantity of salt dissolved does not exceed four or five per cent. It follows from this that the activity of the endosmotic current toward any saline solution will be greatest at the beginning of the experiment and will progressively diminish as the currents continue and the two liquids assume a more nearly uniform density.

The rate of diffusion of different solutions is generally increased by a moderate elevation of temperature.

Bearing in mind these general laws, and remembering that they are applicable to diffusion as it takes place through animal membranes, we can easily understand how different liquids and solutions, in an endosmometer, will attract with different degrees of intensity any given liquid, such as pure water; and how this attractive force, which is measured by the rapidity and extent of the rise of liquid in an endosmometer, may be modified by the concentration of the solution, differences in temperature, and other conditions. The influence which the membrane exerts upon the relative intensity of these currents is dependent to a certain extent upon the diffusion which takes place when the two liquids come together in its substance.

As a rule to which there are not many exceptions, pure water will penetrate animal membranes more readily than any other liquid; and it is consequently from the water to the liquid contained in the endosmometer that the principal current generally takes place. Liquids like alcohol, saline solutions, etc., which have this property, are said to be positively osmotic; while those with which the current takes place in the opposite direction, such as oxalic acid, weak hydrochloric acid, bichloride of platinum, etc., are said to be negatively osmotic. In a series of experiments with different liquids, if the endosmometer be always the same and if all the liquids used be exposed to the action of pure water, in a given time a definite change in the quantity of fluid in the endosmometer will be produced, which will be indicated by a certain amount of elevation or depression in its level.

Applications of Physical Laws to the Function of Absorption.

In no experiments performed out of the body, can the conditions favorable to the passage of liquids through membranes in accordance with purely physical laws be realized as they exist in the living organism. The vast extent of the absorbing surfaces; the great delicacy and permeability of the membranes; the rapidity with which principles are carried on by the torrent of the circulation, as soon as they pass through these membranes; the uniformity of the pressure, notwithstanding the penetration of liquids; all these favor the physical phenomena of absorption in a way which cannot be imitated in artificially-constructed apparatus. It is not necessary to invoke the vital properties of tissues to explain the ordinary phenomena of absorption. Enough has been learned of the laws which regulated endosmosis and exosmosis to enable us to explain most of these phenomena upon physical principles. This fact has been apparent in studying these principles in their relation to absorption in the living body; but it is an important question to determine whether this be applicable to all the varied phenomena of physiological absorption. In other words, are there any modifications in this function which cannot, as yet, be explained by physical laws?

Admitting the fact that the general process of absorption takes place in accordance with the laws of endosmosis, we shall now consider some of the phenomena which appear to be in opposition to known physical principles, or in which the application of these principles seems to be imperfectly understood.

It is not easy to understand how particles of emulsified fat find their way through the walls of the lacteals and blood-vessels, unless we admit the existence of orifices, such as have been described by recent anatomists. The experiments of Matteucci with alkaline emulsions seem to show that alkalinity is a condition necessary to the penetration of fatty particles, although they do not offer an explanation of the mechanism by which these particles pass through membranes. It has been demonstrated that the epithelium which covers these membranes becomes filled with fatty granules during the absorption of emulsions, and some physiologists invoke the aid of "cell-action,"—concerning which it must be confessed that there exists very little definite information—in explanation of this phenomenon. The penetration of fatty particles through membranes must be regarded as one of the points which cannot be explained by the laws of endosmosis.

There are certain experiments on absorption in the living body, to which a great deal of importance was attached by Longet, which are seemingly in opposition to physical laws. This author states that, when solutions of sugar of different densities are secured in isolated portions of the intestine of a living animal, the denser solutions are absorbed with as much rapidity as those which are less concentrated. He also shows that saline solutions of greater density than the blood are absorbed in the living animal, when, according to physical laws, the current should take place in the opposite direction. The view that these facts are in opposition to physical laws is very successfully controverted by Milne-Edwards. This author, referring to some experiments by Von Becker in support of his position, asserts that there is first an exosmosis of the watery portions of the blood to these dense solutions, with a feeble penetration of the solutions into the blood-vessels, until, by the laws of diffusion, the solutions become so diluted as to be readily taken into the circulation. Such an action as this could not take place between two saline solutions in an endosmometer, for both the currents would be equal when the liquids became of equal density; but it has been shown that, after endosmosis in an endosmometer has ceased, it may be again induced by simply agitating the liquids. In physiological absorption, the motion is constant and very rapid, and solutions in their passage along the alimentary canal are continually exposed to fresh absorbing surfaces. Farthermore, the albuminoid matters of the blood, which are very slightly exosmotic, will attract an endosmotic current from liquids even when they are of the same density. The kind of action described by Milne-Edwards would be by no means an isolated example of a liquid passing out of the blood-vessels to be again absorbed after it has acted upon matters contained in the alimentary canal. This takes place with all the digestive fluids; and the liquid is effused, not by simple exosmosis, but by an act of secretion excited by the impression made upon the mucous membrane. We are not justified, therefore, in assuming, with Longet, that the absorption of solutions of greater density than the blood is always in opposition to the laws of endosmosis.

The imbibition of the coloring matter of the bile by the coats of the gall-bladder after death, while nothing of the kind takes place during life, is not due to the absence of so-called vital action. During life, the circulation in the mucous membrane of this reservoir would readily remove the few particles of coloring matter which might penetrate from the bile, and of course there is no time for any coloration to take place.

In treating of the variations and modifications of absorption, we noted an apparent elective power in the mucous membrane of some portions of the alimentary canal. This is illustrated in the failure of the mucous membrane to absorb woorara and various of the animal poisons, which, as a rule, produce their effects only when introduced into a wound or injected into the areolar tissue. The separation of various soluble substances by the process known as dialysis may throw some light upon this subject, but as yet we have no facts which offer a satisfactory explanation of this phenomenon. Certain of these phenomena which show an apparent elective power in absorbing membranes are probably due to a cell-action resembling secretion; for all these surfaces are covered with epithelium, which must be penetrated before the fluids can get to the blood-vessels. But, even with regard to the selection of materials from the blood to form secretions, very little of a definite character is known.

Those who believe that absorption is often modified by so-called vital action offer this in explanation of the important influence of the nervous system upon this function. Precisely how the nervous system affects absorption, in all instances, it is impossible, in the present state of our knowledge, to determine; but modifications are frequently effected through the sympathetic nerves. These nerves, as is well known, are capable of producing important local changes in the circulation, and can even temporarily arrest the capillary circulation in some parts; and it is in this way that many of the variations in absorption may be produced.

Lymph and Chyle.

To complete the history of physiological absorption, it will be necessary to treat of the origin, composition, and properties of the lymph and chyle. It is only within a few years that physiologists have been able to appreciate the importance of the lymph, for the experiments indicating the enormous quantity of this liquid which is continually passing into the blood are of recent date. The earlier experimenters never succeeded in obtaining more than a small quantity of fluid from the lymphatic system. On the other hand, for the long period during which it was supposed that all the products of digestion entered the system by the thoracic duct, the importance of the chyle was much exaggerated; but the researches upon intestinal absorption by Magendie and those who followed him, and the experiments of Colin on the quantity of fluid which passes into the blood by the thoracic duct during the intervals of digestion, have enabled physiologists to form a better estimate of the importance of the lymph and chyle. In studying the properties of these fluids, the consideration of the lymph naturally precedes that of the chyle, as the latter consists simply of lymph, to which certain of the products of digestion have been added by absorption from the alimentary canal.

Mode of obtaining Lymph.—The old methods of obtaining this fluid are no longer employed. In the inferior animals, recently killed, a few drops may be obtained by pricking the lymphatic glands or by exposing the right lymphatic trunk or the thoracic duct and collecting the small quantity of fluid which is discharged when these vessels are punctured. Although a notable quantity of chyle can be obtained from the thoracic duct of an animal killed during intestinal absorption, it is difficult to collect even a small quantity of fluid during the intervals of digestion. Various occasions have presented themselves for obtaining lymph, possessing more or less of its normal characters, from the human subject during life; but, in many of these instances, there existed some pathological condition of the lymphatic system, and it cannot be assumed that the liquid thus obtained was in a perfectly healthy condition.

The first successful experiments in which the lymph and chyle were obtained in quantity were made by Colin. This observer, in operating upon large animals, particularly the ruminants, experienced no great difficulty in isolating the thoracic duct near its junction with the subclavian vein and introducing a metallic tube of sufficient size to allow the free discharge of fluid. These experiments, made upon horses and the larger ruminants, were the first to give any clear idea of the quantity of liquids (lymph and chyle) which pass through the thoracic duct. In an observation upon a cow of medium size, he succeeded in collecting, in the course of twelve hours, the enormous quantity of 105·3 lbs. av. (47,963 grammes); and he farther states that a very much greater amount can be obtained by operating upon ruminants of larger size. Whether this represent the actual quantity which is normally discharged into the venous circulation, is a question which will be considered under the head of the probable quantity of lymph and chyle; but it certainly shows that the lymph cannot but be regarded as one of the most important of the animal fluids.

Among the observations upon the fluids discharged from the thoracic duct, which followed the experiments of Colin, the most interesting are those made in 1859, by Dalton, who operated upon carnivorous as well as herbivorous animals. These experiments were performed upon young goats and dogs, and the general results with regard to the quantity of fluids discharged closely corresponded with those obtained by Colin. The operation of making the fistula in goats is not very difficult, all that is necessary being to cut down upon the subclavian vein at the point where the duct empties into it, and to fix in it a tube of appropriate size; but, in dogs, the vessels are more deeply situated, and the operative procedure is much more tedious. This, however, is the only way in which lymph and chyle can be obtained from the lower animals in any considerable quantity.

Quantity of Lymph.—Although the experiments just described might at first seem sufficient to give a pretty clear idea of the entire quantity of lymph discharged into the venous system, it is evident that the conditions of the circulation of this fluid must be so seriously modified by the establishment of a fistula, that the results thus obtained are far from being entirely satisfactory. In the first place, Colin found that the canal, at its junction with the subclavian vein, was seldom single; and, in many of his observations in which a very large quantity of liquid was obtained, there were several vessels of nearly equal size emptying into the venous system. In the experiment to which we have referred, however, the opening was single; and the quantity of fluid obtained represented all that passed up the thoracic duct during the time that the observation was continued. As we should naturally expect, the discharge of liquid was subject to certain variations, its maximum corresponding with the period of greatest activity in digestion and absorption.

It is not possible to estimate the influence of the unobstructed discharge of lymph and chyle by a fistulous opening upon the absolute quantity which passes out of the canal; and, in the natural course of the circulation, there is a certain amount of obstruction to its entrance into the vein, which might sensibly retard the current.

According to the estimates of Dalton, deduced from his own observations upon dogs and the experiments of Colin upon horses, the total quantity of lymph and chyle produced in the twenty-four hours in a man weighing one hundred and forty pounds is from six to six and a half pounds. And, again, reasoning from experiments made upon dogs eighteen hours after feeding, when the fluid which passes up the thoracic duct may be assumed to be pure, unmixed lymph, the total quantity of lymph alone, produced in the twenty-four hours by a man of ordinary weight, would be between three and a half and four pounds (3·864 lbs.). These estimates can only be accepted as approximative, and they do not indicate the entire quantity of lymph actually contained in the organism.

There are no very satisfactory recent researches with regard to the physiological variations in the quantity of lymph. Collard de Martigny made a series of elaborate investigations a number of years ago, with regard to the effects of starvation upon the constitution and the quantity of the lymph. He found the lymphatics always distended with fluid in dogs killed after two days of total deprivation of food. This condition continued during the first week of starvation; but, after that time, the quantity in the vessels gradually diminished, and, a few hours before death, the lymphatics and the thoracic duct were nearly empty. In comparing the quantity of fluid in the lymphatics of the neck during digestion and absorption with the quantity which they contained soon after digestion was completed, the same observer found that, while digestion and absorption were going on actively, the vessels of the neck contained scarcely any fluid; but the quantity gradually increased after these processes were completed.

Properties and Composition of Lymph.—Lymph taken from the vessels in various parts of the system, or the fluid which is discharged from the thoracic duct during the intervals of digestion, is either perfectly transparent and colorless or of a slightly yellowish or greenish hue. When allowed to stand for a short time, it becomes faintly tinged with red, and frequently it has a pale rose-color when first discharged. Miscroscopical examination shows that this reddish color is dependent upon the presence of a few blood-corpuscles, which are entangled in the clot as the lymph coagulates, thus accounting for the deepening of the color when the fluid has been allowed to stand. The origin of these red corpuscles has long been a subject of discussion. Their constant presence in lymph or chyle discharged by fistulous openings has led to the opinion that they are normal constituents of these fluids; and this view has been adopted without reserve by those who assume that the blood-corpuscles are formed from the white corpuscles, or leucocytes. If this view of the formation of the corpuscular elements of the blood be adopted, there is no good reason why red corpuscles should not be formed from the leucocytes in the lymph and chyle as well as in the blood itself; particularly as the clear fluid of the lymph and chyle contains nearly all the principles found in the plasma of the blood. On the other hand, many physiologists regard the presence of red corpuscles as always accidental; and, in support of this view, Robin brings forward the fact that red corpuscles are never found in lymph taken from a portion of a vessel included between two ligatures. This is certainly a very strong argument against the constant and normal existence of red corpuscles in the lymph, particularly as the connection between the lymphatics and the blood-vessels is very close, and all operations upon the lymphatic system involve disturbances in the circulation. There is no positive evidence of the formation of red corpuscles from the leucocytes; and, if it be the fact that red corpuscles never exist in lymph taken from a portion of a lymphatic vessel included between two ligatures, it is fair to assume that the presence of these corpuscles in lymph and chyle is accidental, and that they are always derived from the blood.

Lymph has no decided or characteristic odor. It is very slightly saline in taste, being almost insipid. Its specific gravity is much lower than that of the blood. Magendie found the specific gravity in the dog to be about 1022. Robin states that the specific gravity of the defibrinated serum of lymph is 1009. In some recent analyses, by Dähnhardt, of the lymph taken from dilated vessels in the leg, in the human subject, the specific gravity was only 1007. The exceedingly low specific gravity in the last instance would rather lead to the opinion that the fluid was not entirely normal. The difficulty in obtaining this fluid in a perfectly normal condition from the human subject has rendered it impossible to ascertain its normal specific gravity, even approximatively; but it evidently possesses a density much inferior to that of the blood. The reaction of the lymph is constantly alkaline.

A few minutes after discharge from the vessels, both the lymph and chyle undergo spontaneous coagulation. According to Colin, the fluid collected from the thoracic duct in the large ruminants coagulates at the end of five, ten, or twelve minutes, and sets into a mass having exactly the form of the vessel in which it is contained. Colin states that the clot is tolerably consistent, but that there is never any spontaneous separation of serum. This may be the fact with regard to the lymph and the chyle of the large ruminants, but, in the observations of Dalton, who operated upon dogs and goats, after a few hours' exposure, the clot contracted to about half its original size, precisely like coagulated blood, expressing a considerable quantity of serum. In one instance, in the dog, the volume of serum, after twenty-four hours of repose, was about twice that of the contracted clot. Milne-Edwards, quoting from an unpublished memoir presented by Colin to the Academy of Sciences, in 1858, states that the lymph does not coagulate in the vessels, even when the circulation is interrupted. This may be the case under ordinary conditions, when the vessels are simply tied; but it was found by Flandrin, that coagulation obstructed the tubes which he introduced into the thoracic duct so completely that he was able to obtain but a small quantity of fluid; a difficulty which is also mentioned by Colin, who states that "the clearing of the tube rarely suffices to reëstablish the flow, for the coagulum formed in the tube is prolonged for a greater or less distance into the interior of the thoracic duct." Coagulation of lymph in the vessels during life, if it occur at all, must be exceedingly infrequent, notwithstanding that the flow of lymph and chyle is very slow and irregular, as compared with the circulation of the blood, and is subject, probably, to frequent interruptions.

Although numerous analyses have been made of lymph from the human subject, the conditions under which the fluid has been obtained render it probable that, in the majority of instances, it was not entirely normal. It will be necessary, therefore, to compare these analyses with observations made upon the lymph of the inferior animals; as, in the latter, this fluid has been collected under conditions which leave no doubt as to its normal character. In the experiments of Colin especially, the fluids taken from the thoracic duct during the intervals of digestion undoubtedly represented the normal, mixed lymph collected from nearly all parts of the body; and the operative procedure in the large ruminants is so simple as to produce little if any general disturbance. The following is an analysis by Lassaigne of specimens of lymph collected by Colin from the thoracic duct of a cow, under the most favorable conditions:

Composition of Lymph from a Cow.

Water	964·0
Fibrin	0·9
Albumen	28·0
Fatty matter	0·4
Chloride of sodium	5·0
Carbonate, phosphate, and sulphate of soda	1·2
Phosphate of lime	0·5
	1,000·0

The proportions given in the table are by no means invariable, the differences in coagulability indicating differences in the proportion of fibrin, and the degree of lactescence showing great variations in the amount of fatty matters. The table may be taken, however, as a pretty close approximation of the average composition of the lymph of these animals, during the intervals of digestion.

The analysis of human lymph which seems to be the most reliable, and in which the fluid was apparently pure and normal, is that of Gubler and Quévenne. The lymph, in this case, was collected by Desjardins from a female who suffered from a varicose dilatation of the lymphatic vessels in the anterior and superior portion of the left thigh. These vessels occasionally ruptured, and the lymph could then be obtained in considerable quantity. When an opening existed, the discharge of fluid could be arrested at will by flexing the trunk upon the thigh. Gubler and Quévenne made elaborate analyses of two different specimens of the fluid, with the following results:

Composition of Human Lymph.

	First analysis.	Second analysis.
Water	939·87	934·77
Fibrin	0·56	0·63
Caseous matter (with earthy phosphates and traces of iron)	42·75	42·80
Fatty matter (in the second analysis, fusible at 102·3° Fahr.)	3·82	9·20
Hydro-alcoholic extract (containing sugar, and leaving, after incineration, chloride of sodium, with the phosphate and the carbonate of soda)	13·00	12·60
	1,000·00	1,000·00

The above analyses show a much larger proportion of solid constituents than was found by Lassaigne in the lymph of the cow. This excess is pretty uniformly distributed throughout all the constituents, with the exception of the fatty matters and fibrin; the former existing largely in excess in the human lymph, especially in the second analysis, while the latter is smaller in quantity than in the lymph of the cow. It is evident, however, from a comparison of the two analyses by Gubler and Quévenne, that the composition of the lymph, even when it is unmixed with chyle, is subject to great variations. The caseous matter given by Gubler and Quévenne is probably equivalent to the albuminous matter of other chemists.

The distinctive characters of the different principles found in the lymph do not demand extended consideration, inasmuch as most of them have already been treated of in connection with the blood. In comparing, however, the composition of the lymph with that of the blood, we are at once struck with the great excess of solid constituents in the latter fluid.

In all analyses, except those of Lhéritier, the organic nitrogenized compounds have been found to be very much less in the lymph than in the blood. This is generally most marked with regard to the elements of fibrin; but, as before stated, the proportion of all these ingredients is quite variable. On account of this deficiency, lymph is much inferior to the blood in coagulability, and the coagulum, when it is formed, is soft and friable. There does not appear, however, to be any actual difference between the coagulating principles of the lymph and of the blood.

Fatty matters have generally been found more abundantly in the lymph than in the blood; but their proportion is even more variable than that of the albuminoid substances.

Very little remains to be said concerning the ordinary inorganic constituents of the lymph. The analyses of Dähnhardt have shown that nearly if not all of the inorganic matters which have been demonstrated in the blood are contained in the lymph; and even a small proportion of iron is given in the analyses by Gubler and Quévenne.

These facts indicate a remarkable correspondence between the composition of the lymph and that of the blood. All of the constituents of the blood, except the red corpuscles, exist in the lymph, the only difference being in their relative proportions.

In addition to the constituents of the lymph ordinarily given, the presence of glucose, and, more lately, the existence of a certain proportion of urea, have been demonstrated in this fluid. It has not been ascertained how the sugar contained in the lymph takes its origin, and its function in this situation is equally obscure.

The presence of urea in considerable quantity in both the chyle and the lymph has been determined by Wurtz; and it is thought by Bernard that the lymph is the principal fluid, if not the only one, by which this excrementitious substance is taken up from the tissues. Although urea always exists in the blood, its quantity is less than in the lymph.

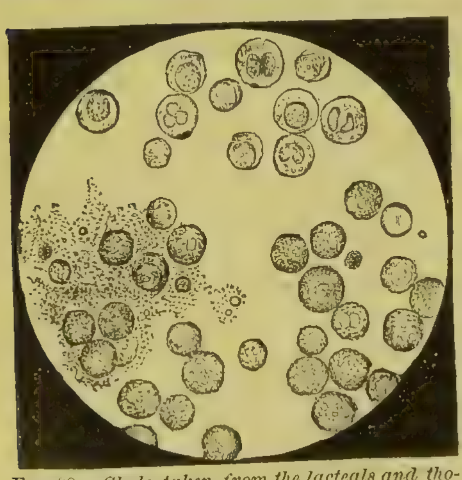


FIG. 98.—*Chyle taken from the lacteals and thoracic duct of a criminal executed during digestion.* (Funke.)
This figure shows the leucocytes and excessively fine granules of fatty emulsion.

Corpuscular Elements of the Lymph.—In every part of the lymphatic system, in addition to a few very minute fatty granules, there are found certain corpuscular elements known as the lymph-corpuscles. These exist, not only in the clear lymph, but in the opaque fluid contained in the lacteals during absorption. They are now regarded as identical with the colorless, globular corpuscles found in the blood, known under the name of white blood-corpuscles, or leucocytes. Although these bodies have been pretty fully described in treating of the corpuscular elements of the blood, they present some peculiarities in the lymphatic system, particularly in their mode of development, which demand consideration.

The leucocytes found in the lymph and chyle are rather less uniform in size and general appearance than the white corpuscles of the blood. Their average diameter is about $\frac{1}{2500}$ of an inch; but some are larger, and others are as small as $\frac{1}{5000}$ of an inch. Some of these corpuscles are quite clear and transparent, presenting but few granulations and an indistinct nuclear appearance in their centre; but others are granular and quite opaque. They present the same adhesive character in the lymph that we have noted in the blood, and frequently they are found collected in masses in different parts of the lymphatic system. Treated with acetic acid, the corpuscles generally become swollen and are rendered very transparent, then presenting from one to four or five nuclear concretions in their interior. In all other regards, these bodies present the same characters as the leucocytes of the blood, and they need not, therefore, be farther described.

We have already alluded to the fact that the lymph-corpuscles are more abundant in the larger than in the smaller vessels, and that they have been thought to be particularly numerous in the vessels coming from the lymphatic glands. It is nevertheless true that corpuscles exist even in the smallest vessels, and they are sometimes quite abundant in lymph which has not passed through the glands. These considerations naturally lead to the theory of the development of leucocytes in the lymphatics, as well as in the ordinary vascular system, particularly as the constant discharge of lymph and chyle into the blood-vessels renders it more than probable that most of the leucocytes found in the blood are derived from the lymph.

The researches of Robin, and of others, by whom his observations have been somewhat extended, have conclusively demonstrated that leucocytes may be developed, under proper conditions, in a clear, structureless blastema, without the intervention of any glandular organ; and, farthermore, it is not necessary that the blastema should be enclosed in any system of vessels. These facts refute completely the idea that the lymph-corpuscles are formed exclusively either by the lymphatic glands or by the walls of the lymphatic vessels. Observations have also shown that leucocytes exist in the blood of the embryon before any lymphatic vessels can be demonstrated; a fact which shows that these bodies may be developed *de novo* in the blood-plasma.

As regards the lymph, there is no fluid in the body which is placed under conditions more favorable to the development of leucocytes. It is enclosed in a system of vessels possessing extremely thin walls and undoubtedly subjected to active osmotic currents. It contains, likewise, a considerable quantity of coagulating matters; and the proportion of these principles has always been found to influence the rapidity of the development of white corpuscles. Its circulation is not very rapid, and the obstacles to the current which are presented in the lymphatic glands undoubtedly give time for the perfection of the structure of leucocytes. It is in this way that the increase in the number of leucocytes as the lymph passes from the periphery to the larger vessels, and especially as the fluid passes through the glands, can be explained.

From the fact that leucocytes are developed before the lymphatic system makes its appearance, that they are found in lymph which has never passed through lymphatic glands, and from observations showing their spontaneous formation in an amorphous blastema, it is the inevitable conclusion that nearly if not quite all of the lymph-corpuscles are developed by genesis in the clear lymph-plasma, and that their development goes on as the fluid circulates toward the venous system. With regard to the influence of the lymphatic glands upon the generation of leucocytes, there is no evidence that the corpuscles which are developed in the course of the lymph through these organs are not here, as elsewhere, formed simply from the blastema; and it is not necessary to invoke any special formative action taking place in the peculiar structures of the glands.

The function of the lymph-corpuscles is obscure. They are discharged into the blood, of which they form a constant constituent. Aside from the hypothesis that they are concerned in the formation of the red blood-disks, no definite and reasonable theory of their physiological office has been proposed.

In addition to the ordinary leucocytes and a certain number of fatty granules, a few small, clear globules or granules, about $\frac{1}{1500}$ of an inch in diameter, called sometimes globulins, are almost constantly present in the lymph. These are insoluble in ether and acetic acid, but are dissolved by ammonia. They are regarded by Robin as a variety of leucocytes and are described by him as free nuclei. They make their appearance in the blastema before the larger leucocytes are developed.

Origin and Function of the Lymph.—There can hardly be any doubt concerning the source of most of the liquid portions of the lymph, for they can be derived only from the blood. Although the exact relations between the smallest lymphatics and the blood-vessels have not been made out in all parts of the system, there is manifestly no anatomical reason why the water, mixed with albuminoid matters and holding salts in solution, should not pass from the blood into the lymphatics; and this is rendered nearly certain if it can be demonstrated that the lymphatics partly or entirely surround many of the blood-vessels, for, under these circumstances, endosmotic and exosmotic currents would inevitably take place. We have seen, in comparing the composition of the lymph with that of the plasma of the blood, that the constituents of these fluids are nearly if not quite identical; the only variations being in their relative proportions. This is another strong argument in favor of the passage of most of the constituents of the blood into the lymph.

One of the most important physiological facts in the chemical history of the lymph is the constant existence of a considerable proportion of urea. This cannot be derived from the blood, for its proportion is greater in the lymph, notwithstanding that this fluid is being constantly discharged into the blood-vessels. The urea which exists in the lymph is derived from the tissues; it is discharged then into the blood, and is constantly being removed from this fluid by the kidneys.

The positive facts upon which to base any precise ideas with regard to the general function of the lymph are not very numerous. From the composition of this fluid, its mode of circulation, and the fact that it is being constantly discharged into the blood, it would not seem to have an important function in the active processes of nutrition. The experiments of Collard de Martigny sustain this view, inasmuch as the quantity and the proportion of solid constituents of the lymph were rather increased than diminished in animals that had been deprived of food and drink for several days; while it is well known that starvation always impoverishes the blood from the first. On the other hand, urea, one of the most important of the products of destructive metamorphosis of the tissues, is undoubtedly taken up by the lymph and conveyed in this fluid to the blood. It remains now for future investigations to determine whether other excrementitious principles may not be taken up from the tissues in the same way—a question of great importance in its relations to the mechanism of excretion.

What is positively known with regard to the functions of the lymph may be summed up in a very few words: A great part of its constituents is evidently derived from the blood, and the relations of these principles to nutrition are not understood. The same may be said of sugar, also a constant constituent of the lymph, the origin of which, even, is not known. Urea and, perhaps, other excrementitious matters are taken up from the tissues by the lymph, and are discharged into the blood, to be removed by the appropriate organs from the system.

While the blood is evidently the great nutritive fluid of the body, being constantly regenerated and purified by the absorption of nutritive matters, by respiration, and by the action of excreting organs, the lymph has an important function in removing from the tissues some, at least, of the products of physiological decay of the organism.

Chyle.

During the intervals of digestion, the intestinal lymphatics and the thoracic duct carry ordinary lymph; but, as soon as absorption of alimentary matters begins, certain nutritive principles are taken up in quantity by these vessels, and their contents are now known under the name of chyle. But little remains to be said concerning this fluid, as we have considered pretty fully the composition and properties of the lymph as well as the different principles taken up by the lacteal vessels which, with the lymph, form the chyle. Some general considerations, however, remain concerning the composition and properties of the chyle as a distinct fluid.

In the human subject and in carnivorous animals, the chyle, taken from the lacteals near the intestine, where it is nearly pure, or from the thoracic duct, when it is mixed with lymph, is a white, opaque, milky fluid, of a slightly saline taste, and an odor which is said to resemble that of the semen. The odor is also said to be characteristic of the animal from which the fluid is taken; although this is not very marked, except on the addition of a concentrated acid, the process employed by Barreul to develop the characteristic odor in the fluids from different animals. Bouisson has found that the peculiar odor of the dog was thus developed in fresh chyle taken from the thoracic duct.

The chyle taken from a fistula into the thoracic duct is frequently of a more or less rosy tint; and it has been a question whether this be due to a peculiar coloring matter or to the accidental presence of a few red blood-corpuscles. Colin, whose experiments in collecting chyle from living animals have been very numerous and successful, assumes that the red coloration is always due to blood-corpuscles coming from the subclavian vein; the valve at the orifice of the thoracic duct not being always sufficient to prevent regurgitation. He has never found blood in the fluid taken from the mesenteric vessels or the receptaculum chyli, and he states, farthermore, that the chyle from these vessels never becomes colored under the influence of the air or of oxygen.

The reaction of the chyle is either alkaline or neutral. Dalton noted an alkaline reaction in the chyle of the goat and of the dog; and a specimen of chyle taken from a criminal immediately after execution, examined by Rees, was neutral. Leuret and Lassaigne obtained the fluid from the receptaculum chyli in a man that had died of cerebral inflammation, and found its reaction to be alkaline.

The specific gravity of the chyle is always less than that of the blood; but it is very variable and depends upon the quality of the food and particularly upon the quantity of liquids ingested. Lassaigne found the specific gravity of a specimen of pure chyle taken from the mesenteric lacteals of a bull to be 1013, and the specific gravity of the specimen of human chyle examined by Rees was 1024.

The differences in the appearance of the chyle in different animals depend chiefly upon the diet. Colin found it excessively milky in the carnivora, especially after fats had been taken in quantity; while, in dogs that were nourished with articles containing but little fat, its appearance was hardly lactescent. Tiedemann and Gmelin found the chyle almost transparent in herbivora fed with hay or straw. They also observed the fact that the chyle was nearly transparent in dogs fed with liquid albumen, fibrin, gelatine, starch, and gluten; while it was white in the same animals fed with milk, meat, bones, etc.

It is impossible to give even an approximative estimate of the entire quantity of pure chyle taken up by the lacteal vessels. When it finds its way into the thoracic duct, it is mingled immediately with all the lymph from the lower extremities; and the immense quantities of fluid which have been collected from this vessel by Colin and others give no idea of the quantity of chyle absorbed from the intestinal canal. We cannot, therefore, attempt to give even an approximate estimate of the absolute quantity of chyle; but it is evident that this is variable, depending upon the nature of the food and the quantity of liquids ingested.

Like the lymph, the chyle, when removed from the vessels, speedily undergoes coagulation. Different specimens of the fluid vary very much as regards the rapidity with which coagulation takes place. The contents of the thoracic duct taken from the inferior animals generally coagulate in a few minutes. The first portion of the fluid collected from the human subject by Dr. Rees (the chyle was collected in this case in two portions) coagulated in an hour. Received into an ordinary glass vessel, the chyle generally separates more or less completely after coagulation into clot and serum, the density and size of the clot indicating the proportion of fibrin. The serum which thus separates is quite variable in quantity and is never clear. Its milkiness does not depend entirely upon the presence of particles of emulsified fat, and it is not rendered transparent by ether. It contains, in addition to these particles, numerous leucocytes and organic granules.

Numerous observations have been made with reference to the influence of different kinds of food upon the chyle; but these have not been followed by any definite results that can be applied to the human subject. It is usual to find the chyle fluid in the lacteals and in the thoracic duct for many hours after death; but it soon coagulates after exposure to the air. Although the entire lacteal system is sometimes found, in the human subject and in the inferior animals, filled with perfectly opaque, coagulated chyle, the fluid does not often coagulate in the vessels.

Composition of the Chyle.—Analyses of the milky fluid taken from the thoracic duct during full digestion by no means represent the composition of pure chyle; and it is only by collecting the fluid from the mesenteric lacteals, that it can be obtained without a very large admixture of lymph. In the human subject, it is rare even to have an opportunity of taking the fluid from the thoracic duct in cases of sudden death during digestion; and, in most of the inferior animals which have been operated upon, it is difficult to obtain fluid from the small lacteals in quantity sufficient for accurate analysis. In operating upon the ox, however, Colin has succeeded in collecting pure chyle in considerable quantity.

The most complete analysis of chyle from the human subject is given by Dr. Rees. The fluid was taken from the thoracic duct of a vigorous man, a little more than an hour after his execution by hanging. The subject was apparently in perfect health up to the moment of his death. The evening before, he ate two ounces of bread and four ounces of meat. At seven o'clock A. M., precisely one hour before death, he took two cups of tea and a piece of toast; and he drank a glass of wine just before mounting the scaffold. When the dissection was made, the body was yet warm, although the weather was quite cold. The thoracic duct was rapidly exposed and divided, and about six fluidrachms of milky chyle were collected. The fluid was neutral and had a specific gravity of 1024. The following was its proximate composition:

Composition of Human Chyle from the Thoracic Duct.

Water	904·8
Albumen, with traces of fibrinous matter	70·8
Aqueous extractive	5·6
Alcoholic extractive, or osmazome	5·2
Alkaline chlorides, carbonates, and sulphates, with traces of alkaline phosphates and oxides of iron	4·4
Fatty matters	9·2
	1,000·0

Of the constituents of the chyle not given in the ordinary analyses, the most important are the urea, which, in all probability, is derived exclusively from the lymph, and sugar, coming from the saccharine and amylaceous articles of food during the digestion of these principles.

The difference in chemical composition between the unmixed lymph and the chyle is very well illustrated in a comparative examination of these two fluids taken from a donkey. The fluids were collected by Mr. Lane, the chyle being taken from the lacteals before reaching the thoracic duct. The animal was killed seven hours after a full meal of oats and beans. The following analyses of the fluids were made by Dr. Rees:

Composition of Chyle and Lymph before reaching the Thoracic Duct.

	Chyle.	Lymph.
Water	902·37	965·36
Albuminous matter	35·16	12·00
Fibrinous matter	3·70	1·20
Animal extractive matter soluble in water and alcohol	3·32	2·40
Animal extractive matter soluble in water only	12·33	13·19
Fatty matter	36·01	a trace
Salts, { Alkaline chlorides, sulphates, and carbonates, with traces of alkaline phosphates, oxide of iron }	7·11	5·85
	1,000·00	1,000·00

The above analyses show a very marked difference in the proportion of solid constituents in the two fluids. The chyle contains about the same proportion of albumen and fibrin as the lymph, with a much larger proportion of salts. The proportion of fatty matters in the chyle is very great, while in the lymph there exists only a trace. The individual constituents of the chyle given in the above tables do not demand any farther consideration than they have already received under the head of lymph. The albuminoid matters are in part derived from the food, and in part from the blood, through the admixture of the chyle with lymph. The fatty matters are derived in greatest part from the food. As far as has been ascertained by analyses of the chyle for salts, this fluid has been found to contain essentially the same inorganic constituents as the plasma of the blood. All of these principles are rapidly poured into the blood, where they assist in supplying the material which is being constantly consumed in the process of nutrition.

The presence of sugar in the chyle was first mentioned by Brande, who described it, however, rather indefinitely. Glucose was distinctly recognized in the chyle by Trommer, and its existence in many of the higher orders of animals has since been fully established by Colin.

Microscopical Characters of the Chyle.—The milky appearance of the chyle as contrasted with the lymph is due to the presence of an immense number of excessively minute fatty granules. The liquid becomes much less opaque when treated with ether, which dissolves many of the fatty particles. In fact, the chyle of the thoracic duct is nothing more than lymph to which an emulsion of fat in a liquid containing albuminoid matters and salts is temporarily added during the process of intestinal absorption. The quantity of fatty granules in the chyle varies considerably with the diet, and it generally diminishes progressively from the smaller to the larger vessels, on account of the constant admixture of lymph. The size of the granules is pretty uniformly from $\frac{1}{25000}$ to $\frac{1}{12500}$ of an inch. They are much smaller and more uniform in size in the lacteals than in the cavity of the intestine. Their constitution is not constant; and they are composed of the different varieties of fat which are taken as food, mingled together in variable proportions.

The ordinary corpuscular elements of the lymph (leucocytes and globulins) are also found in variable quantity in the chyle. These have already been fully considered.

Movements of the Lymph and the Chyle.

Compared with the current of blood, the movements of the lymph and chyle are feeble and irregular; and the character of these movements is such that they are evidently due to a variety of causes. As regards those elements which are derived directly from the blood, the lymph may be said to undergo a true circulation; inasmuch as there is a constant transudation at the peripheral portion of the vascular system, of fluids which are returned to the circulating blood by the communications of the lymphatic system with the great veins. But we have seen that the lymph is not derived entirely from the blood, a considerable portion resulting from interstitial absorption in the general lymphatic system and from the absorption of certain nutritive matters by the chyliferous vessels. These are, physiologically, the most important constituents of the lymph and chyle; and they are taken up simply to be carried to the blood and do not pass again from the general vascular system into the lymphatics.

As far as the mode of origin of the lymph and chyle has any bearing upon the movements of these fluids in the lymphatic vessels, there is no difference between the imbibition of new materials from the tissues or from the intestinal canal, and the transudation of the liquid portions of the blood; for the mechanism of the passage of liquids from the blood-vessels is such that the motive power of the blood cannot be felt. An illustration of this is in the mechanism of the transudation of the liquid portions of the secretions. The force with which fluids are discharged into the ducts of the glands is enormous and is independent of the action of the heart, being due entirely to the force of transudation and secretion. This is combined with the force of imbibition, and with it forms one of the important agents in the movements of the lymph and chyle. These movements are studied with great difficulty. One of the first peculiarities to be observed is, that, under normal conditions, the vessels are seldom distended, and the quantity of fluid which they contain is subject to considerable variation. As far as the flow in the vessels of medium size is concerned, the movement is probably continuous, subject only to certain momentary obstructions or accelerations from various causes. But, in the large vessels situated near the thorax and in those within the chest, the movements are in a marked degree remittent, or they may even be intermittent. All experimenters who have observed the flow of lymph or chyle from a fistula into the thoracic duct have noted a constant acceleration with each act of expiration, and an impulse synchronous with the pulsations of the heart has been frequently observed.

The fact that the lymphatic system is never distended, and the existence of the numerous valves by which different portions may become isolated, render it impossible to estimate the general pressure of fluid in these vessels. This is undoubtedly subject to great variations in the same vessels at different times, as well as in different parts of the lymphatic system. It is well known, for example, that the amount of distention of the thoracic duct is exceedingly variable, its capacity not infrequently being many times increased during active absorption. At the same time it is difficult to attach a manometer to any part of the lymphatic system without seriously obstructing the circulation and consequently exaggerating the normal pressure; but the force with which liquids penetrate these vessels is very great. This is illustrated by the experiment of ligating the thoracic duct; for, after this operation, unless communicating vessels exist by which the fluids can be discharged into the venous system, their accumulation is frequently sufficient to rupture the vessel.

The general rapidity of the current in the lymphatic vessels has never been accurately estimated. As a natural consequence of the variations in the distention of these vessels, the rapidity of the circulation must be subject to constant modifications. Béclard, making his calculation from the experiments of Colin, who noted the quantity of fluid discharged in a given time from fistulous openings into the thoracic duct, estimates that the rapidity of the flow in this vessel is about one inch per second. This estimate, however, can be only approximative; and it is evident that the flow must be much less rapid in the vessels near the periphery than in the large trunks, as the liquid moves in a space which becomes rapidly contracted as it approaches the openings into the venous system.

Causes of the Movements of the Lymph and Chyle.

Various influences combine to produce the movements of fluids in the lymphatic system, some being constant in their operation, and others, intermittent or occasional. These will be considered, as nearly as possible, in the order of their relative importance.

Influence of the Forces of Endosmosis and Transudation (vis a tergo).—The forces of endosmosis and transudation are undoubtedly the main causes of the lymphatic circulation, more or less modified, however, by influences which may accelerate or retard the current; but this action is capable in itself of producing the regular movement of the lymph and chyle. It is a force which is in constant activity, as is seen in cases of ligation of the thoracic duct, an operation which must finally abolish all other forces which aid in producing the lymphatic circulation. When the receptaculum chyli is ruptured as a consequence of obstruction of the thoracic duct, the vessel gives way as the result of the constant endosmotic action, in the same way that the exposed membranes of an egg may be ruptured by endosmosis, when immersed in water.

We have already alluded to the influence of transudation from the blood-vessels and have compared it to the force with which the secretions are discharged into the ducts of the glands; and in placing this, with the force of endosmosis, at the head of the list of the agents which effect the lymphatic circulation, its importance is not over-estimated. This conclusion can hardly be avoided when we consider the anatomy of the lymphatic system. The situations in which the endosmotic force originates are at the periphery, where the single, homogeneous wall of the plexus is excessively thin, and where the extent of absorbing surface is enormous. If liquids can penetrate with such rapidity and force through the walls of the blood-vessels, where their entrance is opposed by the pressure of the fluids already in their interior, they certainly must pass without difficulty through the walls of the lymphatics, where there is no lateral pressure to oppose their entrance, except that produced by the weight of the column of liquid. This pressure is readily overcome; and the numerous valves in the lymphatic system effectually prevent any backward current. The liquid that passes into the lymphatics by endosmosis or by transudation produces movement by displacing an equal bulk of liquid contained in the vessel. We observe with the microscope the rapid filling and rupture of microscopic cells when immersed in water; and the rough experiments by which the operation of endosmosis is ordinarily illustrated, in which the extent of endosmotic surface is infinitely small as compared with that of the lymphatic system, exhibit a current of considerable force and rapidity. When we remember that the infinitely numerous lymphatic radicles are bathed in fluids which undoubtedly pass into their interior with great facility, and when we compare the probable extent of this endosmotic surface with the diameter of the thoracic duct, we can hardly be surprised that this force should be capable of producing a movement in the great trunk at the rate of an inch per second. The great elasticity of the vessels and the fact that they are never completely filled allow of considerable distention of isolated portions of the lymphatic system when there is any obstruction to the current that is not readily overcome. In this way we account for the variations in the flow of the lymph and chyle which are of such constant occurrence.

Influence of the Contractile Walls of the Vessels.—In treating of the anatomy of the lymphatic system, it has already been observed that the large vessels and those of medium size are provided with unstriped muscular fibres and are endowed with contractility. This fact has been demonstrated by physiological as well as anatomical investigations. Béclard states that he has often produced contractions of the thoracic duct by the application of the two poles of an inductive apparatus. It is not uncommon to see the lacteals become reduced in size to a mere thread, even while under observation. Although experiments have generally failed to demonstrate any regular rhythmical contractions in the lymphatic system, it is probable that the vessels contract upon their contents, when they are unusually distended, and thus assist the circulation, the action of the valves opposing a regurgitating current. This action, however, cannot have any considerable and regular influence upon the general current.

Influence of Pressure from Surrounding Parts.—Contractions of the ordinary voluntary muscles, compression of the abdominal organs by contraction of the abdominal muscles, peristaltic movements of the intestines, and pulsations of large arteries situated against the lymphatic trunks, particularly the thoracic aorta, are all capable of increasing the rapidity of the circulation of the lymph and chyle.

The contractions of voluntary muscles assist the lymphatic circulation in precisely the way in which they influence the flow of blood in the venous system; and we have nothing to add regarding this action to what has already been said on this subject in connection with the venous circulation.

Increase in the flow of chyle in the thoracic duct, as the result of compression of the abdominal organs or of kneading the abdomen with the hands, was observed by Magendie, and the fact has been confirmed in all recent experiments on this subject. The same effect, though probably less in degree, is produced by the peristaltic contractions of the intestines.

When a tube is introduced into the upper part of the thoracic duct, it is frequently the case that the fluid is discharged with increased force at each pulsation of the heart. This was frequently observed by Dalton in his experiments on the thoracic duct, and he describes the jets as being "like blood coming from a small artery when the circulation is somewhat impeded." This impulse is due to compression of the thoracic duct as it passes under the arch of the aorta. Its influence upon the general current of the lymph and chyle is probably insignificant, but the fact attracted the attention of Haller, who attached to it a great deal more importance than it is now believed to possess.

Influence of the Movements of Respiration.—While the *vis a tergo* must be regarded as by far the most important agent in the production of the lymphatic circulation, the movements of fluids in the thoracic duct receive constant and important aid from the respiratory acts. This fact has long been recognized; and in the works of Haller will be found a full discussion of the influence of the diaphragm and of the movements of the thorax upon the circulation of chyle. The observations of Colin on this subject are most valuable, as he was the first to successfully establish a fistula into the thoracic duct in large animals. He always found a marked remittency in the flow of chyle from a fistula into the thoracic duct, which was absolutely synchronous with the movements of respiration. With each act of expiration, the fluid was forcibly ejected, and, with inspiration, the flow was very much diminished or even arrested. These impulses became much more marked when respiration was interfered with and the efforts became violent. The intermittency of the current was sometimes so decided, that the pulsations were repeated in a long elastic tube attached to the canula for the purpose of collecting the fluid.

The amount of influence exerted by the respiratory movements upon the flow of the lymph and chyle can be best appreciated by examining carefully the mechanism of its operation.

With each act of inspiration, all the liquids, as well as the air, are drawn toward the cavity of the thorax. In this way, the thoracic duct is dilated and then becomes most distended with fluid. At the same time, the flow of lymph from the right lymphatic duct into the right subclavian vein is increased. After the thoracic duct has been thus dilated in inspiration, at the moment of expiration, in common with all the other parts contained within the thorax, it undergoes compression; the valves prevent the reflux of its contents, and, as a necessary consequence, the fluid is then discharged with increased force into the left subclavian vein. It can be readily understood how the act of inspiration, while it has a tendency to fill the thoracic duct from below, opposes the discharge of fluid from a fistula.

From all these considerations, it is evident that, although there are many circumstances capable of modifying the currents in the lymphatic system, the regular flow of the lymph and chyle depends chiefly upon the *vis a tergo*; but the vessels themselves sometimes undergo contraction, and they are subject to occasional compression from surrounding parts, which, from the existence of numerous valves in the vessels, must favor the current toward the venous system. The alternate dilatation and compression of the thoracic duct with the acts of respiration likewise aid the circulation, and they are more efficient than any other force, except the *vis a tergo*. The action of the valves is precisely the same in the lymphatic as in the venous system.

CHAPTER XI.

SECRETION.

General considerations—Differences between the secretions and fluids containing formed anatomical elements—Classification of the secretions—Mechanism of the production of the true secretions—Mechanism of the production of the excretions—General structure of secreting organs—Anatomical classification of glandular organs—Classification of the secreted fluids—Secretions proper (permanent fluids; transitory fluids)—Excretions—Fluids containing formed anatomical elements—Physiological anatomy of the serous and synovial membranes—Pericardial, peritoneal, and pleural secretions—Synovial fluid—Mucus—Mucous membranes—Mechanism of the secretion of mucus—Composition and varieties of mucus—Microscopical characters of mucus—General function of mucus—Non-absorption of certain soluble substances, particularly venoms, by mucous membranes—Sebaceous fluids—Physiological anatomy of the sebaceous, ceruminous, and Meibomian glands—Ordinary sebaceous matter—Smegma of the prepuce and of the labia minora—Vernix caseosa—Cerumen—Meibomian secretion—Function of the Meibomian secretion—Mammary secretion—Physiological anatomy of the mammary glands—Condition of the mammary glands during the intervals of lactation—Structure of the mammary glands during lactation—Mechanism of the secretion of milk—Conditions which modify the lacteal secretion—Quantity of milk—General characters of milk—Microscopical characters of milk—Composition of milk—Variations in the composition of milk—Colostrum—Lacteal secretion in the newly-born.

Secretion in General.

THE phenomena classed by physiologists under the head of secretion are intimately connected with the general process of nutrition. In the sense in which the term secretion is usually received, it embraces most of the processes in which there is a separation of material from the blood or a formation of a new fluid out of matters furnished by the blood. The blood itself, the lymph, and the chyle, are no longer regarded as secretions. These fluids, like the tissues, are permanent constituents of the organism, undergoing those changes only that are necessary to their proper regeneration. They are likewise characterized by the presence of certain formed anatomical elements, which themselves undergo the processes of molecular destruction and regeneration. These characters are not possessed by the secretions. As a rule, the latter are homogeneous fluids, without formed anatomical elements, except as accidental constituents, such as the desquamated epithelium in mucus or in sebaceous matter. The secretions are not permanent, self-regenerating fluids, except when they perform simply a mechanical function, as the humors of the eye, or the liquids in serous and synovial cavities. They are either discharged from the body, when they are called excretions, or, after having performed their proper function as secretions, are taken up again in a more or less modified form by the blood.

With the exception of those fluids which have a function almost entirely mechanical, the relations of the secretions to nutrition are so close, that the production of many of them forms almost a part of this great function. It is difficult, for example, to conceive of nutrition without the formation of the characteristic constituents of the urine, the bile, and the perspiration; and it is impossible, indeed, to study satisfactorily the phenomena of nutrition without considering fully the various excrementitious principles, such as urea, cholesterine, creatine, creatinine, etc., for the constant formation and discharge of these principles by disassimilation create the necessity for the deposition of new matter in nutrition. Again, the most important of the secretions, as contradistinguished from the excretions, are concerned in the preparation of food by digestion, for the regeneration of the great nutritive fluid.

As would naturally be supposed, the general mechanism of secretion was very imperfectly understood early in the history of physiology, when little was known of the circulation, the functions of the digestive fluids, and particularly of nutrition. From its etymology, the term should signify separation; but it is now known that many of the secreted fluids are formed in the glands and are not simply separated or filtered from the blood. Physiologists now regard secretion as the act by which fluids, holding certain solid principles in solution, and sometimes containing liquid nitrogenized principles, but not necessarily possessing formed anatomical elements, are separated from the blood or are manufactured by special organs out of materials furnished by the blood. These organs may be membranes, follicles, or collections of follicles or tubes. In the latter instance they are called glands. The liquids thus formed are called secretions; and they may be destined to perform some function connected with nutrition or may be simply discharged from the organism.

It is not strictly correct to speak of formed anatomical elements as the results of secretion, except, perhaps, in the case of the fatty particles in the milk. The leucocytes found in pus, the spermatozoids of the seminal fluid, and the ovum, which are sometimes spoken of as products of secretion, are real, anatomical elements developed in the way in which these structures are ordinarily formed. It has been conclusively demonstrated, for example, that leucocytes, or pus-corpuscles, are developed in a clear blastema, without the intervention of any special secreting organ, and that spermatozoids and ova are generated by a true development in the testicles and the ovaries, by a process entirely different from ordinary secretion. It is important to recognize these facts in studying the mechanism by which the secretions are produced. It is true that, in some of the secretions, as the sebaceous matter, a certain quantity of epithelium, more or less disintegrated, is found; but this is to be regarded as an accidental admixture of desquamated matter and not as a product of secretion.

Classification of the Secretions.—The secretions are capable of a physiological classification, dependent upon differences in their functions and in the mechanism of their production. Investigations within the past few years have shown that these differences are very distinct.

Certain of the fluids are formed by special organs, and have important functions to perform which do not involve their discharge from the organism. These may be classed as the true secretions; and the most striking examples of such are the digestive fluids. Each one of these fluids is formed by a special gland or set of glands, which generally has no other function; and they are never produced by any other part. It is the gland which produces the characteristic element or elements of the true secretions out of materials furnished by the blood; and the principles thus formed never preëxist in the circulating fluid. The function which these fluids have to perform is generally intermittent; and, when this is the case, the flow of the secretion is intermittent, taking place only when its action is required. When the parts which produce one of the true secretions are destroyed, as may be sometimes done in experiments upon living animals, the characteristic elements of this particular secretion never accumulate in the blood, nor are they formed vicariously by other organs. The simple effect of such an experiment is absence of the secretion and disturbances consequent upon the loss of its function.

Certain other of the fluids are composed of water, holding one or more characteristic principles in solution, which result from the physiological waste of the tissues. These principles have no function to perform in the animal economy and are simply separated from the blood to be discharged from the body. These may be classed as excretions, the urine being the type of fluids of this kind. The characteristic principles of the excrementitious fluids are formed in the tissues, as one of the results of the constant changes going on in all organized, living structures. They are not produced in the glands by which they are eliminated but appear in the secretion as the result of a sort of elective filtration from the blood. They always preëxist in the circulating fluid and may be eliminated, either constantly or occasionally, by a number of organs. As they are produced continually in the substance of the tissues and are taken up by the blood, they are constantly discharged into the substance of the proper eliminating organs. When the glands which thus eliminate these principles are destroyed or when their functions are seriously impaired, the excrementitious matters may accumulate in the blood and give rise to certain toxic phenomena. These effects, however, are often retarded by the vicarious discharge of such principles by other organs.

There are some fluids, as the bile, which perform important functions as secretions, and which nevertheless contain certain excrementitious matters. In these instances, it is only the excrementitious matters that are discharged from the organism.

In the sheaths of some tendons and of muscles, the substance of muscles, and in some other situations, are found fluids which simply moisten the parts, and which contain very little organic matter, with but a small proportion of inorganic salts. Although these are frequently spoken of as secretions, they are produced generally by a simple, mechanical transudation of certain of the constituents of the blood through the walls of the vessels. Still, it is difficult to draw a line rigorously between transudation and some of the phenomena of secretion; particularly as late experiments upon dialysis have shown that simple, osmotic membranes are capable of separating complex solutions, allowing certain constituents to pass much more freely than others. This fact explains why the transuded fluids do not contain all the soluble principles of the blood in the proportions in which they exist in the plasma. All the secreted fluids, both the true secretions and the excretions, contain many of the inorganic salts of the blood-plasma.

Mechanism of the Production of the True Secretions.—Although the characteristic elements of the true secretions are not to be found in the blood or in any other of the animal fluids, they can generally be extracted in quantity from the glands, particularly during their intervals of repose. This fact has been repeatedly demonstrated with regard to many of the digestive fluids, as the saliva, the gastric juice, and the pancreatic juice; and artificial fluids, possessing many of the physiological properties of the natural secretions, have been prepared by simply infusing the glandular tissue in water. There can be no doubt, therefore, that, even during the periods when the secretions are not discharged, the glands are taking from the blood matters which are to be transformed into principles characteristic of the individual secretions, and that this process is constant. Extending our inquiries into the nature of the process by which these peculiar principles are formed, it is found to bear a close resemblance to the general act of nutrition. There are certain anatomical elements in the glands which have the power of selecting the proper material from the blood and causing them to undergo a peculiar transformation; in the same way that the muscular tissue takes from the great nutritive fluid albuminoid matters and transforms them into its own substance. The exact nature of this property is unexplained. It belongs to the class of phenomena observed in living structures only and is sometimes called vital.

In all of the secreting organs, a variety of epithelium is found, called glandular, which seems to possess the power of forming the peculiar elements of the different secretions. Inasmuch as the epithelial cells lining the tubes or follicles of the glands constitute the only peculiar structures of these parts, the rest being made up of basement-membrane, connective tissue, blood-vessels, nerves, and other structures which are distributed generally in the economy, we should expect that these alone would contain the elements of the secretions. In all probability this is the fact; and, with regard to some of the glands, this has been satisfactorily demonstrated. It has been found, for example, that the liver-cells contain the glycogenic matter formed by the liver; and it has been farther shown that, when the cellular structures of the pancreas have been destroyed, the secretion is no longer produced. There can be hardly any doubt with regard to the application of this principle to the glands generally, both secretory and excretory. Indeed, it is well known to pathologists, that, when the tubes of the kidney have become denuded of their epithelium, they are no longer capable of separating from the blood the peculiar constituents of the urine.

With regard to the origin of the principles peculiar to the true secretions, it is impossible to entertain any other view than that they are produced in the epithelial structures of the glands; and the old idea that they exist ready-formed in the blood cannot be maintained. While the secretions contain inorganic salts in solution, transuded from the blood, the organic constituents, such as pepsin, ptyaline, pancreatine, etc., are readily distinguished from all other albuminoid principles by their peculiar physiological properties; although some of them are apparently identical with albumen in their ultimate composition and in most of their chemical reactions.

It may be stated, then, as a general proposition, that the characteristic elements of the true secretions, as contradistinguished from the excretions, are formed *de novo* by the epithelial structures of the glands, out of material furnished by the blood. Their formation is by no means confined to what is usually termed the period of functional activity of the glands, or the time when the secretions are poured out, but it takes place more or less constantly when no fluid is discharged.

It is more than probable that the formation of the elements of the secretions takes place with fully as much activity in the intervals of secretion as during the discharge of fluid; and most of the glands connected with the digestive system seem to require certain intervals of repose and are capable of discharging their secretions for a limited time only.

When a secreting organ is called into functional activity—like the gastric mucous membrane, or the pancreas, upon the introduction of food into the alimentary canal—a marked change in its condition takes place. The circulation in the part is then very much increased in activity, thus furnishing water and the inorganic elements of the secretion. This difference in the vascularity of the glands during their activity is very marked when the organs are exposed in a living animal and is one of the important facts bearing upon the mechanism of secretion. Beaumont observed this in his experiments on St. Martin and was the first to show conclusively that the gastric juice is secreted only when food is taken into the stomach or when some stimulus is applied to its mucous membrane. Bernard, in his experiments upon the pancreas, noted the pale appearance of the gland during the intervals of digestion and its reddened and congested condition when the secretion flowed from the duct; and these observations have been confirmed by all who have experimented upon the glands in living animals.

In later experiments upon the circulation in the salivary glands and its relation to secretion, Bernard has fully investigated the variations in the vascular supply to the glands, with the most definite and satisfactory results. His observations were made chiefly upon the submaxillary gland in dogs; and he has shown that, during the functional activity of this organ, if a tube be introduced into the vein, the quantity of blood which may be collected in a given time is four or five times that which is discharged in the intervals of secretion. It was ascertained, also, that the venous blood coming from the gland contained much less water than the arterial blood; and, on comparing the quantity of water lost by the blood in its passage through the gland in a given time with the quantity discharged in the saliva, they were found to exactly correspond.

The differences in the quality and the composition of the blood coming from the glands during their repose and their activity have an important bearing upon the mechanism of secretion. As far as the composition is concerned, these differences appear to be dependent mainly upon the modifications in the circulation. When the gland is in repose, the blood coming from it has the usual dark, venous hue and contains the ordinary proportion of carbonic acid; but, during secretion, when the quantity of blood passing through the organ is increased, the color is nearly as bright as that of arterial blood, and the proportion of carbonic acid is very small. At this time, also, the blood is frequently discharged from the vein *pulsatim* to the distance of several inches. The cause of this difference in color is very easily understood. During the intervals of secretion, the blood is sent to the gland for the purposes of nutrition and the manufacture of the elements of the secretion. It then passes through the part in moderate quantity and undergoes the usual change from arterial to venous, in which a great part of the oxygen disappears and carbonic acid is formed; but, when secretion commences, the ordinary nutritive changes are not sufficient to deoxidize the increased quantity of blood, and the venous character of the blood coming from the part is very much less marked. These facts enable us to form a pretty clear idea of the mechanism of secretion; although the exact nature of the forces which effect the changes of the organic principles of the blood into the characteristic elements of the secretions is not understood. Experiments, however, have shown that, in the act of secretion, there are two tolerably distinct processes:

1. It may be assumed that, at all times, the peculiar secreting cells of the glands are forming, more or less actively, the elements of the secretions, which may be washed out of the part or extracted by maceration; but, during the intervals of secretion, the quantity of blood received by the glands is relatively small.

2. In obedience to the proper stimulus, when a gland takes on secretion, the quantity of blood which it receives is four or five times greater than it is during repose. At that time, water, with certain of the salts of the blood in solution, passes into the secreting structure, takes up the characteristic elements of the secretion, and fluid is discharged by the duct.

In all the secretions proper, there are intervals, either of complete repose, as is the case with the gastric juice or the pancreatic juice, or periods when the activity of the secretion is very greatly diminished, as in the saliva. These periods of repose seem to be necessary to the proper performance of the function of the secreting glands; forming a marked contrast with the constant action of the organs of excretion. It is well known, for example, that the function of digestion is seriously disturbed when the act is too prolonged from the habitual ingestion of an excessive quantity of food.

From the considerations already mentioned, it is evident that the secretions, as a rule, are formed by the epithelial structures of the glands. There has been a great deal of speculation with regard to the mechanism of this action of the cells. As we before remarked, this question cannot be considered as settled. It does not seem probable that the cells are ruptured during secretion and discharge their contents into the ducts, for, under these circumstances, we should expect to find some of their structure in the secreted fluid; whereas, aside from accidental constituents, the secretions are homogeneous and do not contain any formed anatomical elements. There is no good reason for supposing that this action takes place and that more or less of the glandular epithelium is destroyed whenever secretion occurs; and, in the present state of our knowledge, we can only assume that the secreting cells induce certain transformations in the organic elements of the blood and modify transudation, without pretending to understand the exact nature of this process.

The theory, that the discharge of the secretions is due simply to mechanical causes and is attributable solely to the increase in the pressure of blood, cannot be sustained. Pressure undoubtedly has considerable influence upon the activity of secretion; but the flow will not always take place in obedience to simple pressure, and secretion may be induced for a limited time without any increase in the quantity of blood circulating in the gland.

The glands possess a peculiar irritability, which is manifested by their action in response to proper stimulation. During secretion, they generally receive an increased quantity of blood; but this is not indispensable, and secretion may be excited without any modification of the circulation. This irritability will disappear when the artery supplying the part with blood is ligated for a number of hours; and secretion cannot then be excited, even when the blood is again allowed to circulate. If the gland be not deprived of blood for too long a period, the irritability is soon restored; but it may be permanently destroyed by depriving the part of blood for a long time. These facts are very striking and they show a certain similarity between glandular and muscular irritability, although their properties are manifested in very different ways.

Mechanism of the Production of the Excretions.—Certain of the glands have the function of separating from the blood excrementitious matters, which are of no use in the economy and are simply to be discharged from the system. These matters, which will be fully considered, both in connection with the fluids of which they form a part and under the head of nutrition, are entirely different in their mode of production from the characteristic elements of the secretions. The formation of excrementitious principles takes place in the tissues and is connected with the general process of nutrition; and in the excreting glands there is simply a separation of matters already formed. The action of the excreting organs being constant, there is not that regular, periodic increase in the activity of the circulation which is observed in secreting organs; but it has been observed that the blood which comes from the kidneys is nearly as red as arterial blood, showing that the quantity of blood which this organ receives is greater than is required for mere nutrition, the excess, as in the secreting organs, furnishing the water and inorganic salts that are found in the urine. It has also been shown that, when the secretion of urine is interrupted, the blood of the renal veins becomes dark, like the blood in the general venous system.

The function of excretion is not, under all conditions, confined to the ordinary excretory organs. When their action is disturbed, certain of the secreting glands, as the follicles of the stomach and intestine, may for a time eliminate excrementitious matters; but this is abnormal and is analogous to the elimination of foreign matters from the blood by the glands.

Influence of the Composition and Pressure of the Blood upon Secretion.—Under normal conditions, the composition of the blood has little to do with the action of the secreting organs, as it simply furnishes the material out of which the characteristic principles of the secretion are formed; but, when certain foreign matters are taken into the system or are injected into the blood-vessels, they are eliminated by the different glandular organs, both secretory and excretory. These organs seem to possess a power of selection in the elimination of different substances. Thus, sugar, ferrocyanide of potassium, and the salts of iron, are eliminated in greatest quantity by the kidneys; the salts of iron, by the kidneys and the gastric tubules; and iodine, by the salivary glands.

The act of secretion is almost always accompanied with an increase in the pressure of blood in the vessels supplying the glands; and it has been shown, on the other hand, that an exaggeration in the pressure, if the nerves of the glands do not exert an opposing influence, increases the activity of secretion. The experiments of Bernard on this point show the influence of pressure upon the salivary and the renal secretion, particularly the latter. After inserting a tube into one of the ureters of a living animal, so that the activity of the renal secretion could be accurately observed, the pressure in the renal artery was increased by tying the crural and the brachial. It was then found that the flow of urine was markedly increased. The pressure was afterward diminished by the abstraction of blood, which was followed by a corresponding diminution in the quantity of urine. The same phenomena were observed in analogous experiments upon the submaxillary secretion. These striking facts, as we have already seen, do not demonstrate that secretion is due simply to an increase in the pressure of blood in the glands, although this undoubtedly exerts an important influence. It is necessary that every condition should be favorable to the act of secretion for this influence to be effective. Experiments have shown that pain is capable of completely arresting the secretion of urine, operating undoubtedly through the nervous system. If the flow of urine be arrested by pain, an increase in the pressure of blood in the part fails to influence the secretion. To illustrate this fact more fully, Bernard divided the nerves on one side, through which the reflex nervous action was communicated to the kidney, leaving the other side intact. He then found that increase in the arterial pressure, accompanied with pain, diminished the flow of urine upon the sound side, through which the nervous action could operate, and increased it upon the other.

The influence of pressure of blood upon secretion may, then, be summed up in a few words: There is always an increase in the activity of secretion when the pressure of blood in the glands is increased, and a diminution when the pressure is reduced; except when there is some modifying influence operating through the nervous system.

Influence of the Nervous System upon Secretion.—The fact that the secretions are generally intermittent in their flow, being discharged in obedience to impressions which are made only when there is a demand for the exercise of their functions, would naturally lead to the supposition that they are regulated, to a great extent, through the nervous system; particularly as it is now well established that the nerves are capable of modifying and regulating local circulations. The same facts apply, to a certain extent, to the excretions, which are also subject to considerable modifications. A few years ago, indeed, there was considerable discussion regarding a subdivision of the reflex system of nerves, which was supposed to preside over secretion and was called the excito-secretory system. The facts which led to the description of this system of nerves had long been observed, and they simply illustrated the production of the secretions in response to irritation.

Experiments have clearly demonstrated the importance of the nervous influence in the production of the secretions; but the observations of Bernard show that the effects are produced mainly by increasing the activity of the circulation in the glands. This takes place in greatest part through filaments from the sympathetic system, which are distributed to the muscular coats of the arteries of supply. When these filaments are divided, the circulation is increased here, as in other situations, and secretion is the result; and, if the extremity of the nerve connected with the gland be galvanized, contraction of the vessels follows, and the secretion is arrested.

With regard to many of the glands, Bernard has shown that the influence of the sympathetic is antagonized by nerves derived from the cerebro-spinal system, which latter he calls the motor nerves of the glands. The motor nerve of the submaxillary is the chorda tympani; and, as both this nerve and the sympathetic, together with the excretory duct of the gland, can be easily exposed and operated upon in a living animal, most of the experiments of Bernard have been performed upon this gland. When all these parts are exposed and a tube is introduced into the salivary duct, division of the sympathetic induces secretion, with an increase in the circulation in the gland, the blood in the vein becoming red. On the other hand, division of the chorda tympani, the sympathetic being intact, arrests secretion, and the venous blood coming from the gland becomes dark. If the nerves be now galvanized alternately, it will be found that galvanization of the sympathetic produces contraction of the vessels of the gland and arrests secretion, while the stimulus applied to the chorda tympani increases the circulation and excites secretion. Enough is known of the nervous influences which modify secretion, to admit of the inference that all the glands are possessed of nerves through which reflex phenomena, affecting their secretions, take place. It is the motor, or functional nerve of the gland through which the reflex action takes place; the influence of the sympathetic being constant and the same as in other parts where it is distributed to blood-vessels.

As reflex phenomena involve the action of a nervous centre, it becomes an interesting question to determine whether any particular parts of the central nervous system preside over the various secretions. We must refer again to the experiments of Bernard for an elucidation of this question. If a puncture be made in the space included between the origin of the pneumogastrics and the auditory nerves, in the floor of the fourth ventricle, there is an increase in the discharge of urine, with an excretion of sugar due to an exaggeration in the sugar-producing function of the liver. Irritation applied a little higher, toward the pons Varolii and just posterior to the origin of the fifth pair of nerves, is followed by a great increase in the activity of the salivary secretion.

Mental emotions, pain, and various circumstances, the influence of which upon secretion has long been observed, operate through the nervous system. Numerous familiar instances of this kind are quoted in works on physiology: such as the secretion of tears; arrest or production of the salivary secretions; sudden arrest of the secretion of the mammary glands, from violent emotion; increase in the secretion of the kidneys or of the intestinal tract, from fear or anxiety; with other examples which it is unnecessary to enumerate.

The effects of destruction of the nerves distributed to the parenchyma of some of the glandular organs are very curious and interesting. Müller and Peipers destroyed the nerves distributed to the kidney and found that, not only was the secretion arrested in the great majority of instances, but the tissue of the kidneys became softened and broken down. These experiments have been repeated by Bernard. He found that animals operated upon in this way died, and that the tissue of the kidney was broken down into a fetid, semifluid mass. After division of the nerves of the salivary glands, the organs became atrophied, but they did not undergo the peculiar putrefactive change which was observed in the kidneys. The same effect was produced when the nerve was paralyzed by introducing a few drops of a solution of woorara at the origin of the little artery which is distributed to the submaxillary gland.

General Structure of Secreting Organs.—In treating of the mechanism of secretion and excretion, it has been evident that all glandular organs must be supplied with blood to furnish the materials for secretion, and be provided with epithelium, which changes these matters into the characteristic elements of the secretions. We can understand how certain of the liquid and saline constituents of the blood can escape by exosmosis through the homogeneous walls of the capillaries, but the more complex secreted fluids require for their formation a different kind of action; although, in the act of secretion, there is considerable transudation of liquid and saline matters, which take up in their course the peculiar principles formed by the cells.

Although it is somewhat difficult to draw a line between transudation and the simplest forms of secretion, it may be assumed, in general terms, that fluids which are exhaled directly from the blood-vessels, without the intervention of glandular apparatus or of a secreting membrane, are transudations; while all fluids produced by simple membranes or by follicles, or which are discharged from the ducts of glands, are secretions. This division places the intermuscular fluid and the fluid found in all soft tissues among the transudations, and the serous and synovial fluids among the secretions.

The serous and synovial membranes present the simplest form of a secreting apparatus. Blood is supplied to them in small quantity, and, on their free surfaces, are arranged one or two layers of epithelial cells which effect the slight changes that take place in the transuded fluids. In some of the serous membranes, as the pleura and peritoneum, the amount of secretion is very small; but others, like the serous pericardium and the synovial membranes, secrete a considerable quantity of fluid. The action of all of these membranes may become exaggerated, as a pathological condition, and the amount of their secretions is then very large.

Anatomists have now a pretty clear idea of the structure of what are called the glandular organs; and it will be seen that they simply present an arrangement by which the secreting surface is increased, and at the same time compressed, as it were, into a comparatively small space. The mucous follicles, for example, are simple inversions of a portion of the mucous membrane; while the ordinary racemose glands are nothing more than collections of follicles around the extremities of excretory ducts. These ideas concerning the general anatomy of the glands date from the observations of Malpighi, who was the first to correct the old notion that the secretions were discharged into the glandular organs through openings in the blood-vessels. It is evident that nothing could have been known of the mechanism of secretion before the connection between the arteries and veins had been ascertained, which, it will be remembered, was also discovered by Malpighi. Although the ideas of Malpighi were not at first generally received, more recent observations with the microscope have shown that they were in the main correct; although, from the imperfection of his optical instruments, Malpighi was unable to investigate very thoroughly the minute structure of the glands.

Anatomical Classification of Glandular Organs.—The organs which produce the different secretions are susceptible of a classification according to their anatomical peculiarities, which greatly facilitates their study. They may be divided as follows:

1. *Secreting membranes.*—Examples of these are the serous and synovial membranes.
2. *Follicular glands.*—Examples of these are the simple mucous follicles, the follicles of Lieberkühn, and the uterine follicles.
3. *Tubular glands.*—Examples of these are the ceruminous glands, the sudoriparous glands, and the kidneys.
4. *Racemose glands, simple and compound.*—Examples of the simple racemose glands are the sebaceous and Meibomian glands, the tracheal glands, and the glands of Brunner. Examples of the compound racemose glands are the salivary glands, the pancreas, the lachrymal glands, and the mammary glands.
5. *Ductless, or blood-glands.*—Examples of these are the thymus, the thyroid, the supra-renal capsules, and the spleen.

The liver is a glandular organ which cannot be placed in any one of the above subdivisions, as we shall see when we come to treat specially of its anatomy. The lymphatic glands and other parts connected with the lymphatic and the lacteal system are not embraced in the above classification. These are sometimes called conglobate glands.

The general structure of secreting membranes and the follicular glands is very simple. The secreting parts consist of a membrane, generally homogeneous, on the secreting surface of which are found epithelial cells, either tesselated or of the variety called glandular. Beneath this membrane, ramify the blood-vessels which furnish the elements of the secretions. The follicular glands are simply digital inversions of this structure, with rounded, blind extremities, the glandular epithelium lining the follicles.

The tubular glands have essentially the same structure as the follicles, except that the tubes are long and are more or less convoluted. The more complex of these organs contain connective tissue, blood-vessels, nerves, and lymphatics.

The compound racemose glands are composed of branching ducts, around the extremities of which are arranged collections of rounded follicles, like bunches of grapes. In addition to the epithelium, basement-membrane, and blood-vessels, these organs contain connective tissue, fibro-plastic elements, lymphatics, involuntary muscular fibres, and nerves. In the simple racemose glands the excretory duct does not branch.

The ductless glands contain blood-vessels, lymphatics, nerves, sometimes involuntary muscular fibres, fibro-plastic elements, and a peculiar structure called pulp, which is composed of fluid with cells and occasionally with closed vesicles. These are sometimes called blood-glands, because they are supposed to modify the blood as it passes through their substance.

The testicles and the ovaries are not simply glandular organs; for, in addition to the production of mucous or watery secretions, their principal function is to develop certain anatomical elements, the spermatozoids and the ova. The physiology of these organs will be considered in connection with the subject of generation

Classification of the Secreted Fluids.—The products of the various glands may be divided, according to their function, into secretions and excretions. The secreted fluids may be subdivided into the permanent secretions, which have a more or less mechanical function, and transitory secretions; some of the latter, like mucus, are thrown off in small quantity, without being actually excrementitious; others, like most of the digestive fluids, are produced intermittently and they rapidly and finally undergo resorption.

Tabular View of the Secreted Fluids.

Secretions Proper.

Permanent Fluids.

Serous fluids.	Vitreous humor of the eye.
Synovial fluid.	Fluid of the labyrinth of the internal ear.
Aqueous humor of the eye.	Cephalo-rachidian, or subarachnoid fluid.

Transitory Fluids.

Mucus, in many varieties.	Saliva.
Sebaceous matter.	Gastric juice.
Cerumen, the waxy secretion of the external meatus.	Pancreatic juice.
Meibomian fluid.	Secretion of the glands of Brunner.
Milk and colostrum.	Secretion of the follicles of Lieberkühn.
Tears.	Secretion of the follicles of the large intestine.
	Bile (also an excretion).

Excretions.

Perspiration and the secretion of the axillary glands.	Urine.
	Bile (also a secretion).

Fluids containing Formed Anatomical Elements.

Seminal fluid, containing, beside spermatozoids, the secretions of a number of glandular structures.
Fluid of the Graafian follicles.

Physiological Anatomy of the Serous and Synovial Membranes.

The serous and synovial membranes, which are frequently classed together by anatomists, present several well-marked points of distinction, both as regards their structure and the products of their secretion. The serous membranes are the arachnoid, pleura, pericardium, peritoneum, and tunica vaginalis testis. The synovial membranes are found around all the movable articulations. They also form elongated sacs enveloping many of the long tendons, and they exist in various parts of the body in the form of shut sacs, when they are called bursæ.

Serous Membranes.—The structure of the serous membranes is very simple. They consist of a dense tissue of fibres, which is frequently quite closely adherent to the subjacent parts, covered by a single layer of pavement, or tesselated epithelium. The fibres are mainly of the inelastic variety, arranged in bundles, interlacing each other in the form of a close net-work, and mingled with small, wavy fibres of elastic tissue and numerous blood-vessels. It has not been satisfactorily demonstrated that the serous membranes contain nerves and lymphatics, although the latter are generally quite abundant in the subjacent parts, particularly beneath the serous membranes covering the viscera. The capillary blood-vessels are in the form of a close, polygonal net-work, with sharp angles. The epithelium of the serous membranes is pale, regular, with rather large nuclei, and is easily detached after death. These membranes, as a rule, form closed sacs, with their opposing or free surfaces nearly in apposition. The secretion, which is generally very small in quantity, is usually contained in their cavity. The exception to this rule is the arachnoid membrane, the surfaces of which are exactly in apposition, the fluid being situated beneath both layers. The peritoneum of the female has an opening on either side for the Fallopian tubes.

Synovial Membranes.—The true synovial membranes are found in the diarthrodial, or movable articulations; but in various parts of the body are found closed sacs, sheaths, etc., which resemble synovial membranes both in structure and in function. Every movable joint is enveloped in a capsule, which is closely adherent to the edges of the articulating cartilage and is even reflected upon its surface for a short distance. It was formerly thought that these membranes, like the serous sacs, were closed bags, with one layer attached to the cartilage and the other passing between the bones so as to enclose the joint; but it is now the general opinion that the cartilage which incrusts the articulating extremities of the bones, though bathed in synovial fluid, is not itself covered by a membrane.

The fibrous portion of the synovial membranes is more dense and resisting and less elastic than the serous membranes. It is composed of white inelastic fibrous tissue, with a few elastic fibres and blood-vessels. The latter are generally not so numerous as in the serous membranes. The internal surface is lined with small cells of flattened pavement-epithelium, with rather large, rounded nuclei. These cells exist in from one to two or four layers.

In most of the joints, especially those of large size, as the knee and the hip, the synovial membrane is thrown into folds which contain a considerable amount of true adipose tissue. In nearly all the joints, the membrane presents fringed, vascular processes, called sometimes synovial fringes. These are composed of looped vessels of considerable size; and when injected they bear a certain resemblance to the choroid plexus. The edges of these fringes present numerous leaf-like, membranous appendages, of a great variety of curious forms. They are generally situated near the attachment of the membrane to the cartilage. There is no reason for supposing that either the adipose folds or the vascular fringes have any special office in the production of the synovial secretion different from that of other portions of the membrane, although such a theory has been advanced.

The arrangement of the synovial bursæ is very simple. Wherever a tendon plays over a bony surface, we find a delicate membrane in the form of an irregularly-shaped, closed sac, one layer of which is attached to the tendon, and the other, to the bone. These sacs are lined with an epithelium like that found in the synovial cavities, and they secrete a true synovial fluid. Numerous bursæ are also found beneath the skin, especially in parts where the integument moves over bony prominences, as the olecranon, the patella, and the tuberosities of the ischium. These sacs, sometimes called bursæ mucosæ, are much more common in man than in the inferior animals and have essentially the same function as the deep-seated bursæ. The form of both the superficial and deep-seated bursæ is very irregular, and their interior is frequently traversed by small bands of fibrous tissue. The synovial sheaths, or vaginal processes, line the canals in which the long tendons play, particularly the tendons of the flexors and extensors of the fingers and toes. They have essentially the same structure as the bursæ, and present two layers, one of which lines the canal, while the other is reflected over the tendon. The vascular folds, described in connection with the articular synovial membranes, are found in many of the bursæ and the synovial sheaths.

Pericardial, Peritoneal, and Pleural Secretions.—In the normal condition of the true serous membranes, the amount of secretion is very small; so small, indeed, that it never has been obtained in quantity sufficient for ultimate analysis. It is not true that these membranes produce merely a vaporous exhalation. Their secretion is always liquid, and, small as it is in quantity, it can be found in the pericardial sac and sometimes in the lower part of the abdominal cavity. As the only apparent function of these fluids is to moisten the membranes so that the opposing surfaces can move over each other without undue friction, only enough fluid is secreted to keep these surfaces in a proper condition. The error frequently committed by authors, in describing the serous exhalations as vaporous, is due to the fact that a vapor is generally given off when the serous cavities are exposed, either in a living animal or in one recently killed. This vaporous exhalation takes place after exposure of the parts; but, if the cavities be observed without exposing the serous surfaces to the air, a certain quantity of liquid can be detected. Colin always found liquid in the peritoneal, pericardial, and pleural cavities of animals recently killed or opened during life. In these cavities, the opposite surfaces of the serous membrane were either in contact or the space between them was filled with liquid. In one of the small ruminants, he removed the muscles and the elastic tunic from the lower part of the abdomen, exposing the transparent peritoneum, and through this membrane he could see liquid collected in the dependent parts.

As far as has been ascertained, the secretions of the different serous membranes bear a close resemblance to each other. They are either colorless or of a slight amber tinge, alkaline in reaction, and have a specific gravity of from 1012 to 1020. Their composition resembles that of the serum of the blood, except that the proportion of water is very much greater. They contain albumen, chlorides, carbonate and phosphate of soda, and a little glucose. These facts are the result of observations upon the serous fluids of some of the inferior animals; and it is exceedingly difficult to obtain the normal fluids from the human subject. The elaborate analyses which are sometimes given of the fluids from the different serous cavities in the human subject are the results of examinations of large morbid accumulations.

The normal quantity of pericardial fluid in the human subject is generally estimated at from one to two fluidrachms. Colin found that the pericardial sac of the horse contained from two and a half to three and a half fluidounces, the cavity being exposed immediately after the death of the animal from hæmorrhage.

The quantity of fluid found in the peritoneal cavity in horses killed in this way was from ten to thirty-four fluidounces.

The quantity of fluid in the pleural cavity in the same animal was from three and a half to seven fluidounces.

These estimates are simply approximative; but they give an idea of the normal quantity of liquid which may reasonably be supposed to exist in the serous cavities of the human subject. Judging from the weight of a man of ordinary size as compared with that of a horse, it may be stated, in general terms, that the pericardial sac contains from two and a half to three and a half fluidrachms; the peritoneal cavity, from one to four fluidounces; and the pleural sac, from three and a half to seven fluidrachms.

The fluid in the cavity of the tunica vaginalis is small in quantity and resembles in every respect the peritoneal secretion. The cephalo-rachidian, or subarachnoid fluid will be described in connection with the anatomy of the cerebro-spinal nervous system.

Synovial Fluid.—Although there is a certain similarity between the serous and the synovial membranes, their secretions differ very considerably in their physical and chemical characters. Like the serosities, the synovial fluid has simply a mechanical function; but it is more viscid and contains a larger proportion of organic matter than the serous fluids. The quantity of fluid in the joints is sufficient to lubricate freely the articulating surfaces. In a horse of medium size and in good condition, examined immediately after death, Colin found 1·6 fluidrachm in the shoulder-joint; 1·9 drachm in the elbow-joint; 1·6 drachm in the coxo-femoral articulation; 2·2 in the femoro-tibial articulation; and 1·9 in the tibio-tarsal articulation.

When perfectly normal, the synovial fluid is either colorless or of a pale, yellowish tinge. It is so viscid that it is with difficulty poured from one vessel into another. This peculiar character is due to the presence of an organic substance called synovine. When this organic matter has been extracted and mixed with water, it gives to the fluid the peculiar viscidity of the synovial secretion. The reaction of the fluid is faintly alkaline, on account of the presence of a small proportion of carbonate of soda. The fluid, especially when the joints have been much used, usually contains in suspension pale epithelial cells and a few leucocytes. The following is the composition of the synovial fluid of the human subject:

Composition of the Synovial Fluid. (Robin.)

Water	928·00
Synovine (called albumen)	64·00
Principles of organic origin (belonging to the second class of Robin)	not estimated.
Fatty matter	0·60
Chloride of sodium, Carbonate of soda	6·00
Phosphate of lime	1·50
Ammonio-magnesian phosphate	traces.

The observations of Frerichs indicate considerable variations in the composition and general characters of the synovial fluid, dependent upon use of the joints. In a stall-fed ox, the proportion of water to solid matter was 969·90 to 30·10; and, in animals that took considerable exercise, the proportions were 948·54 of water to 51·46 of solid matter. In the latter, the fluid was more viscid and contained a larger proportion of synovine with a smaller proportion of salts. It was also more deeply colored and contained a larger number of leucocytes.

Like the serous fluids, the synovial secretion is produced by the general surface of the membrane and not by any special organs. The folds and fringes which have been described were at one time supposed to be most active in secreting the organic matter, but there is no evidence that they have any such special office.

The aqueous humor of the eye and the fluid of the labyrinth of the internal ear resemble the serous secretions in many regards; but these fluids, with the vitreous humor, will be considered in connection with the physiological anatomy of the eye and ear.

Mucus.

Mucous Membranes.—The mucous membranes in different situations present important peculiarities in structure, many of which have already been considered. We have described in detail the mucous membrane of the air-passages and of the alimentary canal, in connection with the subjects of respiration and digestion; and the membranes in other parts will necessarily be described in treating of the physiology of the organs in which they are found. It will be sufficient at present to take a general view of the structure of these membranes and the mechanism of the production of the various fluids known under the name of mucus.

A distinct anatomical division of the mucous membranes may be made into two classes, as follows: First, those provided with pavement-epithelium; and second, those provided with columnar or conoidal epithelium. All of the mucous membranes line cavities or tubes communicating with the exterior by the different openings in the body.

The following are the principal situations in which the first variety of mucous membranes, covered with pavement-epithelium, are found: The mouth, the lower part of the pharynx, the œsophagus, the conjunctiva, the female urethra, and the vagina. In these situations, the membrane is composed of a chorion made up of inelastic and elastic fibrous tissue, a few fibro-plastic elements, with capillaries, lymphatics, and nerves. The elastic fibres are small and quite abundant. The membrane itself is loosely united to the subjacent parts by areolar tissue. The chorion is provided with vascular papillæ, more or less marked; but, in all situations, except in the pharynx, the epithelial covering fills up the spaces between these papillæ, so that the membrane presents a smooth surface. Between the chorion and the epithelium, is an amorphous basement-membrane. The mucous glands open upon the surface of the membrane by their ducts, but the glandular structure is situated in the submucous areolar tissue. These glands have many of them been described in connection with the mucous membrane of the mouth, pharynx, and œsophagus. They are generally simple racemose glands, presenting a collection of follicles arranged around the extremity of a single excretory duct, lined or filled with rounded, nucleated epithelium. The pavement-epithelium covering these membranes exists generally in several layers, and presents great variety, both in form and size. The most superficial layers are of large size, flattened, and irregularly polygonal. The deeper layers are smaller and more rounded. The size of these cells is from $\frac{1}{2500}$ to $\frac{1}{300}$ of an inch. The cells are pale, slightly granular, and possess a small, ovoid nucleus, with one or two nucleoli.

The second variety of mucous membranes, covered with columnar epithelium, is found lining the alimentary canal below the cardiac orifice of the stomach, the biliary passages, the excretory ducts of all the glands, the nasal passages, the upper part of the pharynx, the uterus and Fallopian tubes, the bronchi, the Eustachian tubes, and the male urethra. In certain situations, this variety of epithelium is provided on its free surface with little hair-like processes called cilia. During life the cilia are in constant motion, producing a current generally in the direction of the mucous orifices. Ciliated epithelium is found throughout the nasal passages, commencing about three-quarters of an inch within the nose; in the upper part of the pharynx; the posterior surface of the soft palate; the Eustachian tube; the tympanic cavity; the larynx, trachea, and bronchial tubes, until they become less than $\frac{1}{50}$ of an inch in diameter; the neck and body of the uterus; the Fallopian tubes; the internal surface of the eyelids; and the ventricles of the brain. This variety of mucous membrane is formed of a chorion, a basement-membrane, and epithelium. The chorion is composed of inelastic and elastic fibres, with fibro-plastic elements, a few unstriped muscular fibres, amorphous matter, blood-vessels, nerves, and lymphatics. It is less dense and less elastic than the chorion of the first variety and is generally more closely united to the subjacent tissue. The surface of these membranes is generally smooth, the only exception being the mucous membrane of the pyloric portion of the stomach and the small intestines. These membranes are provided with follicular glands, extending through their entire thickness and terminating in rounded extremities, sometimes single and sometimes double, which rest upon the submucous structure. Many of them are provided also with simple racemose glands, the ducts passing through the membrane, the glandular structure being situated in the submucous areolar tissue. The columnar epithelium covering these membranes rests upon an amorphous structure, called basement-membrane. It generally presents but few layers, and sometimes, as in the intestinal canal, there is only a single layer. The cells are prismoidal, with a large, free extremity, and a pointed end which is attached. The lower strata of cells are shorter and more rounded than those in the superficial layer. The cells are pale, very closely adherent to each other by their sides, and provided with a moderate-sized, oval nucleus with one or two nucleoli. The length of the cells is from $\frac{1}{500}$ to $\frac{1}{700}$ of an inch, and their diameter, from $\frac{1}{5000}$ to $\frac{1}{2500}$ of an inch. When villosities exist on the surface of the membranes, the cells follow the elevations and do not fill up the spaces between them, as in most of the membranes covered with pavement-epithelium.

The mucous membrane of the urinary bladder, the ureters, and the pelvis of the kidneys, cannot be classed in either of the above divisions. They are covered with mixed epithelium, presenting all varieties of form between the pavement and the columnar, some of the cells being caudate and quite irregular in shape.

Mechanism of the Secretion of Mucus.—Nearly every one of the great variety of fluids known under the name of mucus is composed of the products of several different glandular structures. According to Robin, mucus proper is produced by the epithelial cells of that portion of the membrane situated on the surface, between the opening of the so-called mucous follicles or glands; while the secretion of these special glandular organs always possesses peculiar properties. It is undoubtedly true that certain membranes which do not possess glands, as the mucous lining of the ureters and a great portion of the urinary bladder, are capable of secreting mucus. The mucous membrane of the stomach produces an alkaline, viscid secretion, during the intervals of digestion, when the gastric glands do not act; and the gastric glands, during digestion, secrete a fluid of an entirely different character. The fluid produced by the follicles of the small intestine likewise has peculiar digestive properties. These circumstances, and the fact that the entire extent of the mucous membranes is covered with more or less secretion, show that the general epithelial covering of these membranes is capable of secreting a fluid which forms one of the constituents of what is ordinarily recognized as mucus. It is impossible, however, to separate the secretion of the superficial layer of cells from the other fluids that are found on the mucous membranes; and it will be more convenient to regard as mucus, the secretion which is found upon mucous membranes, except when, as in the case of the gastric or the intestinal juice, we can recognize a special fluid by certain distinctive physiological properties.

In the membranes covered with cylinder-epithelium, which are usually provided with numerous simple follicles, the secretion is produced mainly by these follicles, but in part by the epithelium covering the general surface. The membranes covered with pavement-epithelium usually contain but few follicles and are provided with simple racemose glands situated in the submucous structure, which are to be regarded rather as appendages to the membrane. The secretion is here produced by the epithelium on the free surface and is always mixed with fluids resulting from the action of the mucous glands.

There is nothing to be said with regard to the mechanism of the secretion of mucus beyond what has already been stated in connection with the general mechanism of secretion. All the mucous membranes are quite vascular, and the cells covering the membrane and lining the follicles and glands attached to it have the property of taking from the blood the materials necessary for the formation of the secretion. These principles pass out of the cells upon the surface of the membrane in connection with water and inorganic salts in variable proportion. Many of the cells themselves are desquamated and are found in the secretion, together with a few leucocytes, which are produced upon mucous surfaces with great facility.

Composition and Varieties of Mucus.—In comparing the secretions of the different mucous membranes, each one will be found to possess certain distinctive peculiarities, more or less marked; but there are certain general characters which belong to all varieties of mucus. The fluid is usually a mixture of the secretion from the simple membrane and the product of its follicles or glandular appendages and always contains a certain amount of desquamated epithelium; and it is frequently possible, from the microscopical characters of the epithelium, to indicate the part from which any given specimen of mucus has been taken. This desquamation of epithelium must not be regarded as a necessary condition of the secretion of mucus, any more than the desquamation of the epidermic scales is to be regarded as a condition necessary to the secretion of perspiration or sebaceous matter. It is a property of the epidermis and the epithelial covering of mucous membranes to be regenerated by the formation of new cells from below, the effete structures being thrown off, and the admixture of these with mucus is simply accidental. The leucocytes, formerly called mucus-corpuscles, are the result of irritation of the mucous membrane and are not constant constituents of normal mucus.

All the varieties of mucus are more or less viscid; but this character is very variable in the secretions from different membranes, in some of them the secretion being quite fluid, and in others, almost semisolid. The different kinds of mucus vary considerably in general appearance. Some of them are perfectly clear and colorless; but the secretion is generally grayish and semitransparent. Examined by the microscope, in addition to the mixture of epithelium and the occasional leucocytes, which give to the fluid its semi-opaque character, the mass of the secretion presents a very finely-striated appearance, as though it were composed of thin layers of a nearly transparent substance, with many folds. These delicate striæ do not usually interlace with each other, and they are rendered more distinct by the action of acetic acid. This appearance, with the peculiar effect of the acid, is characteristic of mucus. Some varieties of mucus present very fine, pale granulations and a few small globules of oil.

On the addition of water, mucus is somewhat swollen but is not dissolved. An exception to this is the secretion of the conjunctival mucous membrane, which is coagulated on the addition of water. As a rule, the reaction of mucus is alkaline; the only exception to this being the vaginal mucus, which is very fluid and is distinctly acid.

It is exceedingly difficult to get an exact idea of the proximate composition of normal mucus, from the fact that the quantity secreted by the membranes in their natural condition is very small, being just sufficient to lubricate their surface. All varieties, however, contain a peculiar organic principle, called mucosine, which gives to the fluid its peculiar viscidity. They likewise present a considerable variety of inorganic salts, as the chlorides of sodium and potassium, alkaline lactates, carbonate of soda, phosphate of lime, a small proportion of the sulphates, and, in some varieties, traces of iron and silica. Of all these constituents, mucosine is the most important, as it gives to the secretion its characteristic properties. Like all other organic nitrogenized principles, mucosine is coagulable by various reagents. It is imperfectly coagulated by heat; and, after desication, it can be made to assume its peculiar consistence by the addition of a small quantity of water. It is coagulated by acetic acid and by a small quantity of the strong mineral acids, being redissolved in an excess of the latter. It is also coagulated by strong alcohol, forming a fibrinous clot soluble in hot and cold water. Mucosine may be readily isolated by adding water to a specimen of normal mucus, filtering, and precipitating with an excess of alcohol. If this precipitate, after having been dried, be exposed to water, it assumes the viscid consistence peculiar to mucosine. This property serves to distinguish it from albumen and other organic nitrogenized principles.

Nasal Mucus.—The nasal mucus, being subject to so many changes from irritation of the Schneiderian membrane, presents considerable variation in its appearance and composition. Under perfectly normal conditions, it is very viscid, clear or slightly opaque and grayish, and strongly alkaline. It always contains more or less columnar epithelium. In its behavior in the presence of various reagents, it presents the characteristics which we have ascribed to the secretions of the mucous membranes generally. The following is the composition of the normal secretion:

Composition of Nasal Mucus. (Robin.)

Water	933·00	to	947·00
Mucosine (with a trace of albumen ?)	53·30	"	54·80
Lactate of soda (?)	1·00	"	5·00
Organic crystalline principles	2·00	"	1·05
Fatty matters and cholesterine	not estimated.		5·01
Chlorides of sodium and potassium	5·60	to	5·09
Calcareous and alkaline phosphates	3·50	"	2·00
Sulphate and carbonate of soda	0·90	not estimated.	

Bronchial and Pulmonary Mucus.—This is the secretion of the general mucous surface of the larynx and bronchial tubes, mixed with the products of the glands situated in the substance of these membranes and in the submucous tissue. In addition to this secretion, there is an exhalation of watery vapor containing traces of organic matter, coming from the air-cells and the bronchial tubes less than $\frac{1}{50}$ of an inch in diameter, which are not provided with mucous glands. This variety of mucus is alkaline and is quite similar to nasal mucus in its appearance and general characters.

Mucus secreted by the Mucous Membrane of the Alimentary Canal.—Throughout the alimentary canal, from the mouth to the anus, the lining membrane secretes a certain quantity of mucus, which does not differ very much from the mucus found in other situations. This secretion appears to take place independently of the act of digestion, and the mucus in most parts of the tract is not known to possess any peculiar digestive properties. By ligating all of the salivary ducts, the buccal mucus has been procured. This secretion is produced by the cells covering the general surface of the membrane and is mixed with the secretion of the isolated follicular and racemose glands of the mouth. An analogous secretion is produced by the mucous membrane of the pharynx and œsophagus. During the intervals of digestion, a viscid, alkaline secretion covers the mucous membrane of the stomach. The digestive secretions of the small intestine are so viscid that it has been found impossible to separate them from the true mucous secretion; but undoubtedly a secretion of ordinary mucus is constantly taking place from the lining membrane of both the small and the large intestine. This secretion probably has a purely mechanical function, serving to lubricate the membranes and facilitate the movements of the opposing surfaces against each other.

The mucous membrane of the gall-bladder produces quite an abundant secretion; but this is always mixed with the bile, and it will be considered in connection with the composition of this fluid, although it is not known to possess any peculiar properties.

Mucus of the Urinary Passages.—A small quantity of mucus is secreted by the urinary passages. This is present in the normal urine, in the form of a very slight, cloudy deposit, which forms after the urine has been allowed to stand for a few hours. A certain amount of secretion takes place from the mucous membrane of the bladder, which, as we have seen, does not possess glands except near the neck. This secretion is produced in very small quantity, and it may be recognized in the urine by the ordinary microscopical characters of mucus.

Mucus of the Generative Passages.—The vagina secretes a small quantity of mucus, which differs from the secretions of the other mucous membranes in being distinctly acid and almost entirely wanting in viscidity. The mucus of the neck of the uterus is clear, viscid, and distinctly alkaline. This is ordinarily produced in small quantity, but it is very abundant during pregnancy. It is the result of the action chiefly of the large, rounded glands found in this situation. The mucus of the body of the uterus and of the Fallopian tubes is alkaline, of a grayish color, and slightly viscid. The secretions of these parts are greatly modified during menstruation. These considerations, however, belong properly to the subject of generation and will be taken up more fully hereafter.

Conjunctival Mucus.—A small quantity of a viscid secretion constantly covers the conjunctival mucous membrane, and this is a mixture of the secretion of the membrane itself with the fluid produced by the little mucous glands found near the internal angle of the eye. A peculiarity of this variety of mucus is that it becomes white, like coagulated albumen, by the action of pure water. A peculiarity of the mucus from the conjunctiva, the urethra of the male, and the vagina, is that they readily become virulent when secreted in abnormal quantity. They then contain a large number of leucocytes and have a more or less puriform character.

General Function of Mucus.—The smooth, viscid, and adhesive character of mucus, forming, as this fluid does, a coating for the mucous membranes, serves to protect these parts, enables their surfaces to move freely one upon the other, and modifies to a certain extent the process of absorption. This function is entirely independent of the function of some of the mucous glands, as the follicles of Lieberkühn, which produce secretions only at particular times.

Aside from the mechanical functions of mucus, it has been shown that this fluid, in connection with the epithelial covering of the mucous membranes, is capable of preventing the absorption of certain substances. It is well known, for example, that venoms may be applied with impunity to certain mucous surfaces, while they produce poisonous effects if introduced into the circulation. These agents are not neutralized by the secretions of the parts, for they will produce their characteristic effects upon the system when removed from the mucous surfaces and introduced into the circulation; and it is reasonable to suppose that the mucous membranes are capable of resisting their absorption. This fact is proven by the following interesting experiment, detailed by Robin:

Let an endosmometer be constructed, using a fresh mucous membrane, on the surface of which the epithelium and layer of mucus remain intact, and in the interior of the apparatus, place a saccharine solution, and let the membrane be exposed to a solution containing some venomous fluid. The liquid will mount in the interior of the apparatus, but the poison will not penetrate the membrane. If the mucus and epithelium be now removed with the finger-nail from even a small portion of the membrane, the poison will immediately pass through that part of the membrane, and an animal may be killed with the fluid which now penetrates into the interior of the endosmometer.

These facts show that mucus is an important secretion. It not only has a useful mechanical function, but it is in all probability closely connected with some of the phenomena of elective absorption which are so often observed, particularly in the alimentary canal.

Sebaceous Fluids.

The general cutaneous surface is constantly lubricated by a small quantity of a peculiar, oily secretion, called sebum, or sebaceous matter. This secretion is somewhat modified in certain situations, and an analogous fluid is produced by special glands opening into the external meatus of the ear. Another fluid, very much like the ordinary sebaceous matter, is smeared upon the edges of the eyelids. These secretions, called respectively cerumen and Meibomian fluid, resemble the secretion of the ordinary sebaceous glands sufficiently to be classed with it.

Physiological Anatomy of the Sebaceous, Ceruminous, and Meibomian Glands.—The true sebaceous glands are found in all parts of the body that are provided with hair; and, as nearly every part of the general surface presents either the long, the short, or the downy hairs, these glands are very generally distributed. They exist, indeed, in greater or less numbers in all parts of the skin, except the palms of the hands and the soles of the feet. In the labia minora in the female, and in portions of the prepuce and glans penis of the male, parts not provided with hair, small, racemose sebaceous glands are found, which produce secretions differing somewhat from that formed by the ordinary glands. The glands in the areola of the nipple in the female are very large and are connected with small, downy hairs.

Nearly all of the sebaceous glands are either simple racemose glands, that is, presenting a number of follicles connected with a single excretory duct, or compound racemose glands presenting several ducts, with their follicles, opening by a common tube. Although there is this variation in the size and arrangement of the glands of the general surface, they secrete essentially the same fluid, and their anatomical differences consist simply in a multiplication of follicles.

The differences in the size of the sebaceous glands bear a certain relation to the size of the hairs with which they are connected; and, as a rule, the largest glands are connected with the small, downy hairs. These distinctions in size are so marked, that the glands may be divided into two classes; viz., those connected with the long hairs of the head, face, chest, axilla, and genital organs, and the coarse, short hairs, and those connected with the fine, downy hairs.

The glands connected with the larger hair-follicles are of the simple racemose variety and are from $\frac{1}{120}$ to $\frac{1}{40}$ of an inch in diameter. From two to five of these glands are generally found arranged around each hair-follicle. They discharge their secretion at about the junction of the upper third with the lower two-thirds of the hair-follicle. The follicles of the long hairs of the scalp are generally provided each with a pair of sebaceous glands, measuring from $\frac{1}{120}$ to $\frac{1}{75}$ of an inch in diameter. Encircling the hairs of the beard, the chest, axilla, and genital organs, are large glands, some of them $\frac{1}{40}$ of an inch in diameter, arranged in groups of from four to eight.

The glands connected with the follicles of the small, downy hairs are so large, as compared with the hair-follicles, that the latter seem rather as appendages to the glandular structures. These glands are of the compound racemose variety and present sometimes as many as fifteen *culs-de-sac*. The largest are found on the nose, the ear, the caruncula lachrymalis, the penis, and the areola of the nipple, where they measure from $\frac{1}{50}$ to $\frac{1}{12}$ of an inch. The glands connected with the downy hairs of other parts are usually smaller. The glands of Tyson, situated upon the corona of the glans penis and behind, upon the cervix, are sebaceous glands of the compound racemose variety.

FIG. 99.—*Sebaceous glands.* (Sappey.)

A, a gland in its most rudimentary form: 1, rudimentary hair-follicle; 2, downy hair; 3, simple sebaceous follicle. B, a gland more developed: 1, hair-follicle; 2, simple sebaceous follicle. C, a gland with two follicles: 1, hair-follicle; 2, simple follicle; 3, follicle imperfectly divided. D, a compound gland: 1, hair-follicle; 2, lobule with three follicles; 3, lobule with four follicles. E, a gland with four lobules: 1, hair-follicle; 2, 2, first lobule; 3, second lobule; 4, 4, third lobule; 5, fourth lobule; 6, excretory duct with a hair passing through it. F, a gland with four lobules: 1, hair-follicle; 2, 2, first lobule; 3, second lobule; 4, third lobule; 5, fourth lobule; 6, excretory duct.

The minute structure of the sebaceous glands is very simple. The follicles which compose the simple glands and the follicular terminations of the simple and compound racemose glands are formed of a delicate, structureless or slightly granular membrane, with an external layer of inelastic and small elastic fibres, and are lined by cells. Next the membrane, the cells are polyhedric, pale, and granular, most of them presenting a nucleus and a nucleolus; but the follicle itself contains fatty granules and the other constituents of the sebaceous matter, with cells filled with fatty particles. These cells abound in the sebaceous matter as it is discharged from the duct. The great quantity of fatty granules and globules found in the ducts and follicles of the sebaceous glands renders them dark and opaque when examined with the microscope by transmitted light, and their appearance is quite distinctive. The larger glands are surrounded with capillary blood-vessels. The glands which open into the larger hair-follicles will be illustrated in connection with the anatomy of the hairs.

The ceruminous glands of the ear produce a secretion resembling the sebaceous matter in many regards, but in their anatomy they are almost identical with the sudoriparous glands. They belong to the variety of glands called tubular, and they consist of a nearly straight tube which penetrates the skin and a rounded or ovoid coil situated in the subcutaneous structure. These glands are found only in the cartilaginous portion of the external meatus, where they exist in great numbers. They are rather more numerous in the inner than in the outer half of the meatus.

The ducts of the ceruminous glands are short and nearly straight, simply penetrating the different layers of the skin, and are from $\frac{1}{700}$ to $\frac{1}{500}$ of an inch in diameter. Their openings are rounded and about $\frac{1}{270}$ of an inch in diameter. They sometimes terminate in the upper part of one of the hair-follicles. They present an external coat of white fibrous tissue and are lined with several layers of small, pale, nucleated epithelial cells.

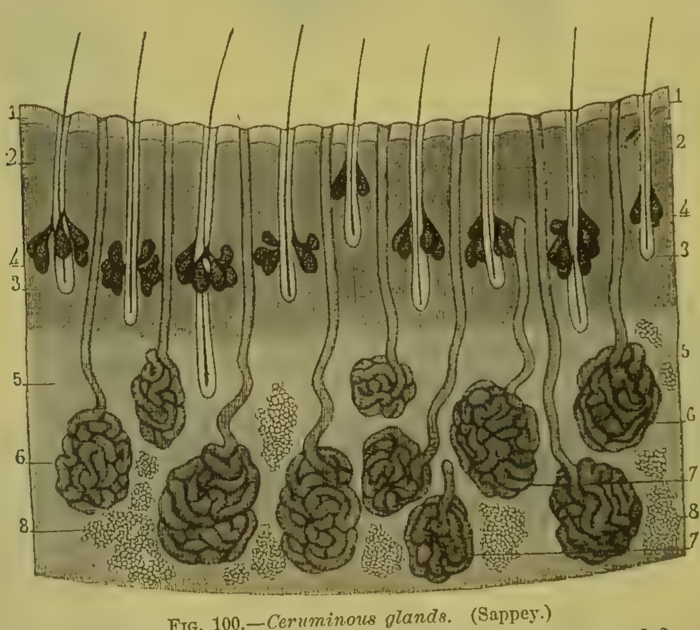


FIG. 100.—*Ceruminous glands.* (Sappey.)

Vertical section of the skin of the external auditory meatus: 1, 1, epidermis; 2, 2, derma; 3, 3, series of hair-follicles lodged in the substance of the skin; 4, 4, series of sebaceous glands attached to these follicles; 5, 5, subcutaneous areolar layer; 6, 6, ceruminous glands; 7, 7, ceruminous glands with the ducts divided; 8, 8, adipose vesicles.

The glandular coil is an ovoid or rounded, brownish mass, from $\frac{1}{120}$ to $\frac{1}{50}$ or $\frac{1}{16}$ of an inch in diameter. It is simply a convoluted tube, continuous with the excretory duct and terminating in a somewhat dilated, rounded extremity. It presents, occasionally, small, lateral protrusions. The diameter of the tube is from $\frac{1}{300}$ to $\frac{1}{250}$ of an inch. It possesses a fibrous coat, with a longitudinal layer of involuntary muscular fibres, and externally a few elastic fibres. It is lined by a single layer of irregularly polygonal cells, which are from $\frac{1}{2000}$ to $\frac{1}{1200}$ of an inch in diameter. These cells contain numerous brownish or yellowish pigmentary granules. The tube forming the gland contains a clear fluid mixed with a granular substance containing cells.

In addition to the ceruminous glands of the ear, numerous sebaceous follicles are found connected with the hair-follicles here, as in other parts provided with hair. The arrangement of the ordinary sebaceous glands and the ceruminous glands, which are situated in different planes in the subcutaneous structure, is shown in Fig. 100.

The Meibomian glands of the eyelids have essentially the same structure as the ordinary sebaceous glands. Their ducts, however, are longer, and the terminal follicles are arranged in a peculiar manner by the sides of the tubes along their entire length. These glands are situated partly in the substance of the tarsal cartilages, between their posterior surfaces and the conjunctival mucous membrane. They are placed at right angles to the free border of the eyelids, opening upon the inner edge and occupying the entire width of the cartilages. From twenty-five to thirty glands are found in the upper, and from twenty to twenty-five, in the lower lid.

Each Meibomian gland consists of a nearly straight excretory duct, from $\frac{1}{300}$ to $\frac{1}{240}$ of an inch in diameter, communicating laterally with numerous compound racemose acini, or collections of follicles, measuring from $\frac{1}{300}$ to $\frac{1}{120}$ of an inch. From fifteen to twenty of these collections of follicles are found on either side of the duct in glands of medium length. Most of the excretory ducts are nearly straight, but some are turned upon themselves near their upper extremity. The general arrangement of these glands is shown in Fig. 101.

In general structure there is little if any difference between the terminal follicles of the Meibomian glands and the follicles of the ordinary sebaceous glands. They are lined with cells measuring from $\frac{1}{2400}$ to $\frac{1}{1200}$ of an inch in diameter. These cells contain numerous fatty globules, but they do not coalesce into large drops, such as are often seen in the ordinary sebaceous cells. The follicles and ducts are filled with the whitish, oleaginous matter which constitutes the Meibomian secretion, or the sebum palpebrale.

In addition to the Meibomian secretion, the edges of the palpebral orifice receive a small amount of secretion from ordinary sebaceous glands of the compound racemose variety (ciliary glands), which are appended in pairs to each of the follicles of the eyelashes, and from the sebaceous glands attached to the small hairs of the caruncula lachrymalis.

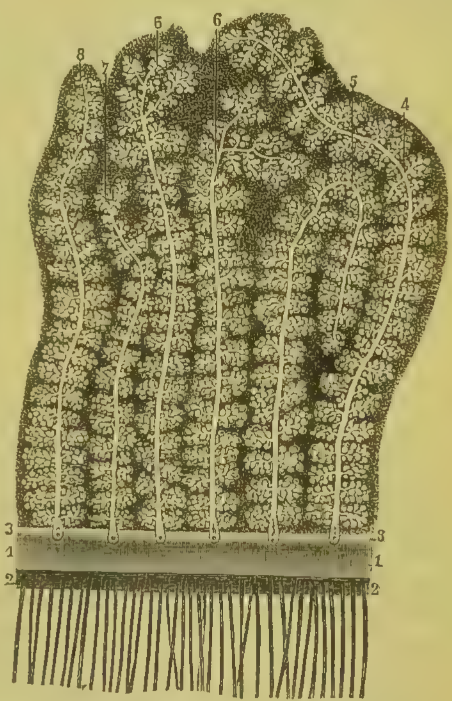


FIG. 101.—*Meibomian glands of the upper lid; magnified 7 diameters.* (Sappey.)

1, 1, free border of the lid; 2, 2, anterior lip penetrated by the eyelashes; 3, 3, posterior lip, with the openings of the Meibomian glands; 4, a gland passing obliquely at the summit; 5, another gland bent upon itself; 6, 6, two glands in the form of racemose glands at their origin; 7, a very small gland; 8, a medium-sized gland.

Ordinary Sebaceous Matter.—Although it may be inferred, from the great number of sebaceous glands opening upon the cutaneous surface, that the amount of sebaceous matter must be considerable, it has been impossible to collect the normal fluid in quantity sufficient for ultimate analysis. In certain parts, as the skin of the nose, where the glands are particularly abundant, a certain amount of oily secretion is sometimes observed, giving to the surface a greasy, glistening aspect. This may be absorbed by paper, giving it the well-known appearance produced by oily matters, and it may be collected in small quantity upon a glass slide and examined microscopically. It then presents a number of strongly-refracting fatty globules, with a few epithelial cells. The cells, however, are not numerous in the fluid as it is discharged upon the general surface; but, if the contents of the ducts and follicles be examined, cells will here be found in great abundance. Most of the cells, indeed, remain in the glands, and the oily matter only is discharged. The object of this secretion is to lubricate the general cutaneous surface and to give to the hairs that softness which is characteristic of them when in a perfectly healthy condition.

It is only when the action of the sebaceous glands has become more or less modified, that the secretion can be obtained in sufficient quantity for chemical analysis; but we cannot be certain that the fluid taken under these conditions is perfectly normal. The analysis by Esenbeck, which is often quoted in works on physiology, was the result of an examination of the contents of a largely-distended hair-follicle; and, as the secretion was confined for a long time, it is evident that it must have undergone material alteration. We cannot, indeed, refer to any ultimate analysis of the normal sebaceous secretion; but, of all the examinations that have been made of the secretion when it has been considerably increased in quantity, those of Lutz give the best idea of what may be supposed to be nearly its ordinary composition. This observer analyzed the secretion in a case of general hypertrophy of the sebaceous system. The fluid which he extracted from the dilated glands was milky-white, and of about the consistence, when cold, of wax. The mean of eight analyses of this fluid was as follows:

Composition of Sebaceous Matter.

Water	357
Oleine	270
Margarine	135
Butyric acid and butyrate of soda	3
Caseine	129
Albumen	2
Gelatine	87
Phosphate of soda and traces of phosphate of lime	7
Chloride of sodium	5
Sulphate of soda	5
	1,000

This analysis gives the proportions of animal and solid matters, desiccated in a current of dry air. Robin, who has reviewed at considerable length the analytical process employed by Lutz, regards the matter supposed to be either caseine or some analogous albuminoid substance, as the organic matter of the epithelial cells that exist in such great numbers in distended sebaceous glands. He regards the weight of the substances designated under the names of albumen, caseine, and gelatine, with a certain quantity of the water driven off by desiccation, as representing the proportion of epithelium. This view is very reasonable, as the microscope always shows in these collections great numbers of epithelial cells. Cholesterine, which is present so frequently in the contents of sebaceous cysts, does not exist in the normal secretion, nor was it found in the analyses by Lutz.

During the latter months of pregnancy and during lactation, the sebaceous glands of the areola of the nipple become considerably distended with a grayish-white, opaque secretion, containing numerous oily globules and granules. Frequently the fluid contains also a large number of epithelial cells. During the periods above indicated, the secretion here is always much more abundant than in the ordinary sebaceous glands.

Smegma of the Prepuce and of the Labia Minora.—In the folds of the prepuce of the male and on the inner surface and folds of the labia minora in the female, a small quantity of a whitish, grumous matter, of a cheesy consistence, is sometimes found, particularly when proper attention is not paid to cleanliness. The matter which thus collects in the folds of the prepuce has really little analogy with the ordinary sebaceous secretion. Examination with the microscope shows that it is composed almost entirely of irregular scales of pavement-epithelium, which do not present the fatty granules and globules usually observed in the cells derived from the sebaceous glands. Robin regards the production of this substance as entirely independent of the secretion of sebaceous matter, as it is formed chiefly in parts of the prepuce in which the sebaceous glands are wanting.

The smegma of the labia minora is of the same character as the smegma preputiale; but it contains drops of oil and the other products of the sebaceous glands found in these parts.

Vernix Caseosa.—The surface of the fœtus at birth and near the end of gestation is generally covered with a whitish coating, or smegma, called the vernix caseosa. This is most abundant in the folds of the skin; but it usually covers the entire surface with a coating of greater or less thickness and of about the consistence of lard. There are great differences in fœtuses at term as regards the quantity of the vernix caseosa. In some the coating is so slight that it would not be observed unless on close inspection. There are few analyses giving an accurate view of the ultimate composition of this substance; and we can form the best idea of its constitution and mode of formation from microscopical examinations. If a small quantity be scraped from the surface and be spread out upon a glass slide with a little glycerine and water, it will be found, on microscopical examination, to consist of an immense number of epithelial cells, with a very few small, fatty granules. In the following table, it is seen that these cells, after desiccation, constituted about ten per cent. of the entire mass. The fatty granulations are very few and do not seem to be necessary constituents of the vernix, as they are of the sebaceous matter. In fact, the vernix caseosa must be regarded as the residue of the secretion of the sebaceous glands, rather than an accumulation of true sebaceous matter.

Composition of the Vernix Caseosa. (Robin.)

Water	769·80 to 778·70
Nitrogenized matter, mucous or caseous	4·50
Desiccated epithelium	101·30
Cholesterine, Oleine and margarine, Oleates and margarates of potassa and of soda,	108·25
Chloride of sodium, Hydrochlorate of ammonia, Phosphate of soda and of lime, Ammonio-magnesian phosphate,	14·95

The function of the vernix caseosa is undoubtedly protective. If we attempt to make a microscopical preparation of the cells with water, it becomes evident that the coating is penetrated by the liquid with very great difficulty, even when mixed with it as thoroughly as possible. Indeed, we never observe at birth the peculiar effects of prolonged contact of the cutaneous surface with water. The protecting coat of vernix caseosa allows the skin to perform its functions in utero, and, at birth, when this coating is removed, the surface is found in a condition perfectly adapted to extra-uterine existence. It is not probable that the vernix caseosa is necessary to facilitate the passage of the child into the world, for the parts of the mother are always sufficiently lubricated with mucous secretion.

Cerumen.—A peculiar substance of a waxy consistence is secreted by the glands that have been described in the external meatus, under the name of ceruminous glands, mixed with the secretion of sebaceous glands connected with the short hairs in this situation. It is difficult to ascertain what share these two sets of glands have in the formation of the cerumen. Robin is of the opinion that the waxy portion of the secretion is produced entirely by the sebaceous glands, and that the convoluted glands, commonly known as the ceruminous glands, produce a secretion like the perspiration. He calls the latter, indeed, the sudoriparous glands of the meatus. This view is, to a certain extent, reasonable; for the sebaceous matter is not removed from the meatus by friction, as in other situations, and would have a natural tendency to accumulate. But the contents of the ducts of the ceruminous glands differ materially from the fluid found in the ducts of the ordinary sudoriparous glands, containing granules and fatty globules, such as exist in the cerumen. Although the glands of the ear are analogous in structure, and, to a certain extent, in the character of their secretion, to the sudoriparous glands, the fluid which they produce is peculiar. We shall see, also, that the perspiratory glands of the axilla and of some other parts produce secretions differing somewhat from ordinary perspiration. As far as can be ascertained, the cerumen is produced by both sets of glands. The sebaceous glands attached to the hair-follicles probably secrete most of the oleaginous and waxy matter, while the so-called ceruminous glands produce a secretion of much greater fluidity, but containing a certain amount of granular and fatty matter.

The consistence and general appearance of cerumen are quite variable within the limits of health. When first secreted, it is of a yellowish color, about the consistence of honey, becoming darker and much more viscid upon exposure to the air. It has a very decided and bitter taste. It readily forms a sort of emulsive mixture with water.

Examined microscopically, the cerumen is found to contain semisolid, dark granulations of an irregularly polyhedric shape, with epithelium from the sebaceous glands, and epidermic scales, both isolated and in layers. Sometimes, also, a few crystals of cholesterine are found.

Chemical examination shows that the cerumen is composed of oily matters fusible at a low temperature, a peculiar organic matter resembling mucosine, with salts of soda and a certain quantity of phosphate of lime. The yellow coloring matter is soluble in alcohol; and the residue after evaporation of the alcohol is very soluble in water and may be precipitated from its watery solution by the neutral acetate of lead or the chloride of tin. This extract has an exceedingly bitter taste.

The cerumen lubricates the external meatus, accumulating in the canal around the hairs. Its peculiar bitter taste is supposed to be efficient in preventing the entrance of insects.

Meibomian Secretion.—Very little is known concerning any special properties of the Meibomian fluid, except that it mixes with water in the form of an emulsion more readily than the other sebaceous secretions. It is produced in small quantity, mixed with a certain amount of mucus and the secretion from the ordinary sebaceous glands attached to the eyelashes (ciliary glands) and the glands of the caruncula lachrymalis, and smears the edges of the palpebral orifice. This oily coating on the edges of the lids, unless the tears be produced in excessive quantity, prevents their overflow upon the cheeks and directs the excess of fluid into the nasal duct.

Mammary Secretion.

The mammary glands are among the most remarkable organs in the economy; not only from the peculiar character of their secretion, which is unlike the product of any other of the glands, but from the great changes which they undergo at different periods, both in size and structure. Rudimentary in early life, and in the male at all periods of life, these organs are fully developed in the adult female, only in the latter months of pregnancy and during lactation. It is true that, in the female, after puberty, the mammary glands undergo a marked and rapid increase in size; but even then they are not fully developed, and, if examined with the microscope, they are found to lack the essential anatomical characters of secreting organs. The physiological anatomy of the mammary glands consequently possesses peculiar interest, aside from the great importance of their secretion.

It will be found convenient to consider these organs in three stages of development; viz., in their rudimentary condition, as they exist in the male and in the female before puberty; in the partially-developed state, as they are found in the unimpregnated female after puberty and during the intervals of lactation; and, finally, in the fully-developed condition, when milk is secreted.

Physiological Anatomy of the Mammary Glands.

The form, size, and situation of the mammæ in the adult female are too well known to demand more than a passing mention. These organs are almost invariably double and are situated on the anterior portion of the thorax, over the great pectoral muscles. In women who have never borne children, they are generally firm, nearly hemispherical, with the nipple at the most prominent point. In women who have borne children, the glands, during the intervals of lactation, are usually larger, are held more loosely to the subjacent parts, and are apt to become flabby and pendulous. The areola of the nipple is also darker.

In both sexes, the mammary glands are nearly as fully developed at birth as at any time before puberty. They make their appearance at about the fourth month, in the form of little elevations of the structure of the true skin, which soon begin to send off processes beneath the skin, which are destined to be developed into the lobes of the glands. In the fœtus at term, the glands measure hardly more than one-third of an inch in diameter. At this time, there are from twelve to fifteen lobes in each gland, and each lobe is penetrated by a duct, with but few branches, composed of fibrous tissue and lined with columnar epithelium. The ends of these ducts are frequently somewhat dilated; but what have been called the gland-vesicles do not make their appearance before puberty. In the adult male, the glands are from half an inch to two inches broad, and from $\frac{1}{12}$ to $\frac{1}{4}$ of an inch in thickness. In their structure, however, they present little if any difference from the rudimentary glands of the infant.

As the period of puberty approaches in the female, the rudimentary ducts of the different lobes become more and more ramified. Instead of each duct having but two or three branches, the different lobes, as the gland enlarges, are penetrated by innumerable ramifications, which have gradually been developed as processes from the main duct. It is important to remember, however, that these branches are never so numerous or so long during the intervals of lactation as they are when the organ is in full activity. The ordinary condition of the gland, as compared with its structure during activity, is one of atrophy.

Condition of the Mammary Glands during the Intervals of Lactation.—At this time the glands are not secreting organs. They present the ducts, ramifying, to a certain extent, in the substance of the lobes into which the structure is divided, but their branches are short and possess but few of the glandular acini that are observed in every part of the organs during lactation. This difference in the structure of the glands is most remarkable; and, as they pass from a secreting to a non-secreting condition at the end of lactation, the ducts retract in all their branches, and most of the secreting *culs-de-sac* disappear. At this time, the glandular tissue is of a bluish-white color and loses the granular appearance which it presents during functional activity. The ducts are then lined with a small, nucleated, pavement-epithelium, which is not found during the secretion of milk. These changes, pointed out by Robin, whose observations have been verified and extended by Sappey, are confined almost exclusively to the secreting structure of the glands. The interstitial tissue remains about the same, the blood-vessels, only, being increased in number during lactation.

Structure of the Mammary Glands during Lactation.—Between the fourth and the fifth month of utero-gestation, the mammary glands begin to increase in size; and, at term, they are very much larger than during the unimpregnated state. At this time, the breasts become quite hard, and the surface near the areola is somewhat uneven, from the great development of the ducts. The nipple itself is increased in size, the papillæ upon its surface and upon the areola are more largely developed, and the areola becomes larger, darker, and thicker. The glandular structure of the breasts during the latter half of pregnancy becomes so far developed, that, if the child be born at the seventh month, the lacteal secretion may generally be established at the usual time after parturition. Even when parturition takes place at term, a few days elapse before secretion is fully established, and the first product of the glands, called colostrum, is very different from the fully-formed milk.

The only parts of the covering of the breasts that present any peculiarities are the areola and the nipple. The surface of the nipple is covered with papillæ, which are very largely developed near the summit. It is covered by epithelium in several layers, the lower strata being filled with pigmentary granules. The true skin covering the nipples is composed of inelastic and elastic fibres, containing a large number of sebaceous glands, but no hair-follicles or sudoriparous glands. According to Sappey, these glands, which are from eighty to one hundred and fifty in number, are always of the racemose variety, and they never exist in the form of simple follicles, as they are described by most anatomists. The nipple contains the lactiferous ducts, fibres of inelastic and elastic tissue, with an immense number of non-striated muscular fibres. The muscular fibres have no definite direction, but are so numerous that, when they are contracted, the nipple becomes very firm and hard. The nipple, although it may thus become hard upon the application of cold or other stimulus, presents none of the anatomical characteristics of the true erectile organs, as is erroneously supposed by some authors; and its hardening is simply due to contraction of its muscular fibres.

The areola does not lie, like the general integument covering the gland, upon a bed of adipose tissue, but it is closely adherent to the subjacent glandular structure. The skin here is much thinner and more delicate than in other parts, and the pigmentary granules are very abundant in some of the lower strata of epidermic cells, particularly during pregnancy. The true skin of the areola is composed of inelastic and elastic fibres and lies upon a distinct layer of non-striated muscular fibres. The arrangement of the muscular fibres (sometimes called the subareolar muscle) is quite regular, forming concentric rings around the nipple. These fibres are supposed to be useful in compressing the ducts during the discharge of milk. The areolar presents the following structures: numerous papillæ, considerably smaller than those upon the nipple; hair-follicles, containing small, rudimentary hairs; sudoriparous glands; and sebaceous glands connected with the hair-follicles. The sebaceous glands in this situation are very large, and their situation is indicated by little prominences on the surface of the areola, which are especially marked during pregnancy.

The mammary gland itself is of the compound racemose variety. It is covered in front by a subcutaneous layer of fat, and posteriorly it is enveloped in a fibrous membrane loosely attached to the pectoralis major muscle. A considerable amount of adipose tissue is also found in the substance of the gland between the lobes.

Separated from the adipose and fibrous tissue, the mammary gland is found divided into lobes, from fifteen to twenty-four in number. These, in their turn, are subdivided into lobules made up of a greater or less number of acini, or *culs-de-sac*. The secreting structure is of a reddish-yellow color and is distinctly granular, presenting a decided contrast to the pale and uniformly fibrous appearance of the gland during the intervals of lactation. If the ducts be injected from the nipple and be followed into the substance of the gland, each one will be found distributing its branches to a distinct lobe; so that the organ is really made up of a number of glands, in their structure identical with each other. It will be most convenient, in studying the intimate structure of the gland, to begin at the nipple and follow out one of the ducts to the termination of its branches in the secreting *culs-de-sac*.

The canals which discharge the milk at the nipple are called lactiferous or galactophorous ducts. They vary in number from ten to fourteen. The openings of the ducts at the nipple are very small, measuring only from $\frac{1}{60}$ to $\frac{1}{40}$ of an inch. As each duct passes downward, it enlarges in the nipple to $\frac{1}{25}$ or $\frac{1}{12}$ of an inch in diameter, and beneath the areola it presents an elongated dilatation, from $\frac{1}{6}$ to $\frac{1}{3}$ of an inch in diameter, called the sinus of the duct. During lactation, a considerable quantity of milk collects in these sinuses, which serve as reservoirs. Beyond the sinuses, the caliber of the ducts measures from $\frac{1}{12}$ to $\frac{1}{8}$ of an inch. They penetrate the different lobes, branching and subdividing, to terminate finally in the collections of *culs-de-sac* which form the acini. Most modern observers are agreed that there is no anastomosis between the different lactiferous ducts, and that each one is distributed independently to one or more lobes.

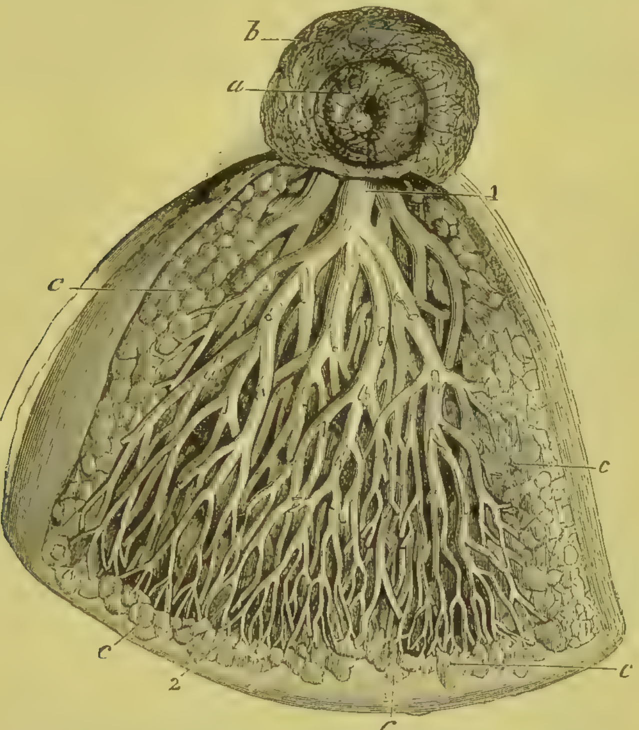


FIG. 102.—*Mammary gland of the human female.* (Liégeois.)
a, nipple, the central portion of which is retracted; *b*, areola; *c*, *c*, *c*, *c*, *c*, lobules of the gland: 1, sinus, or dilated portion of one of the lactiferous ducts; 2, extremities of the lactiferous ducts.

The intimate structure of the lactiferous ducts is interesting and important. They are possessed of three distinct coats. The external coat is composed of anastomosing fibres of elastic tissue, with some inelastic fibres. The middle coat is composed of non-striated muscular fibres, arranged longitudinally and existing throughout the duct, from its opening at the nipple to the secreting *culs-de-sac*. The internal coat is an amorphous membrane, lined with roundish or elongated cells during the intervals of lactation and even during pregnancy, but deprived of epithelium during the period when the lacteal secretion is most active.

The acini of the gland, which are very numerous, are visible to the naked eye, in the form of small, rounded granules, of a reddish-yellow color. Between these acini, there exist a certain quantity of the ordinary white fibrous tissue and quite a number of adipose vesicles. The presence of adipose tissue in considerable quantity in the substance of the glandular structure is peculiar to the mammary glands. Each acinus is made up of from twenty to forty secreting vesicles, or *culs-de-sac*. These vesicles are irregular in form, often varicose, and sometimes they are enlarged and imperfectly bifurcated at their terminal extremities. During lactation, their diameter is from $\frac{1}{400}$ to $\frac{1}{300}$ of an inch. During pregnancy, and when the gland has just arrived at its full development, the secreting vesicles are formed of a structureless membrane, lined with small, nucleated cells of pavement-epithelium. The nuclei are relatively large, ovoid, and are embedded in a small amount of amorphous matter, so that they almost touch each other. Sometimes the epithelium is segmented, and sometimes it exists in the form of a continuous nucleated sheet. When the secretion of milk becomes active, the epithelium entirely disappears, and it reappears as the secretion diminishes. This observation is due to Robin and has an important bearing upon the mechanism of the secretion of milk.

During the intervals of lactation, as the lactiferous ducts become retracted, the glandular *culs-de-sac* disappear; and, in pregnancy, as the gland takes on its full development, the ducts branch and extend themselves, and the vesicles are gradually developed around their terminal extremities. These changes in the development of the mammæ at different periods are most remarkable and are not observed in any other of the glandular organs.

Mechanism of the Secretion of Milk.—With the exception of water and inorganic principles, all the important and characteristic constituents of the milk are formed in the substance of the mammary glands. The secreting structures have the property of separating from the blood a great variety of inorganic principles; and we shall see, when we come to study the composition of the milk more minutely, that it furnishes all the inorganic matter necessary for the nutrition of the infant, containing, even, a small quantity of iron. Precisely how the secreting vesicles separate the proper quantity of these principles from the circulating fluid, we are unable, in the present state of our knowledge, to state. It is unsatisfactory enough to say that the membranes of the vesicles have an elective action, but this expresses the extent of our information on the subject.

The lactose, or sugar of milk, the caseine, and the fatty particles, are all produced *de novo* in the gland. The peculiar kind of sugar here found does not exist anywhere else in the organism. Even when the secretion of milk is most active, different varieties of sugar, such as glucose or cane-sugar, injected into the blood-vessels of a living animal, are never eliminated by the mammary glands, as they are by the kidneys; and their presence in the blood does not influence the quantity of lactose found in the milk. All that can be said with regard to the formation of sugar of milk is that it is produced in the mammary glands. The mechanism of its formation is not understood.

Caseine is produced in the mammary glands, probably by a peculiar transformation of the albuminoid constituents of the blood. This principle does not exist in the blood, although its presence here has been mentioned by some observers. It is well known that the caseine of milk is precipitated by an excess of sulphate of magnesia; but the so-called caseine of the blood is not affected by this salt and passes through it like albumen.

The fatty particles of the milk are likewise produced in the substance of the gland, and the peculiar kind of fat which exists in this secretion is not found in the blood. The mechanism of the production of fat in the mammary glands is obscure. The particles are not produced in cells and set free by their rupture, by a process analogous to that which takes place in the formation of the fatty particles found in the sebaceous matter, for, during the time when the secretion of milk is most active, the epithelium of the secreting *culs-de-sac* has entirely disappeared. The butter is produced by the action of the amorphous walls of the vesicles, in the same way, probably, as fat is produced by the vesicles of the ordinary adipose tissue. At least, this is all that is known regarding the mechanism of its production.

As regards the mechanism of the formation of the peculiar and characteristic constituents of the milk, the mammary glands are to be classed among the organs of secretion and not with those of elimination or excretion; for none of these elements preëxist in the blood, and they all appear first in the substance of the glands.

During the period of secretion, the glands receive a much larger supply of blood than at other times. Pregnancy favors the development of the secreting portions of the glands but does not induce secretion. On the other hand, when pregnancy occurs during lactation, it diminishes, modifies, and it may arrest the secretion of milk. The secretion is destined, however, for the nourishment of the child and not for use in the economy of the mother—an important point of distinction from all other secretions—and its production presents one or two interesting peculiarities.

In the first place, the secreting action of the mammary glands is nearly continuous. When the secretion of milk has become fully established, while there may be certain periods when it is formed in greater quantity than at others, there is no absolute intermittency in its production.

Again, in all the other glandular organs, the epithelial cells found in their secreting portion seem to be the active agents in the production of the secretions; but, in the mammary glands, as we have already noted, the epithelium entirely disappears from the secreting *culs-de-sac* during the period of greatest functional activity of the gland, and nothing is left to perform the work of secretion but the amorphous membrane of the vesicles.

Conditions which modify the Lacteal Secretion.—Very little is known concerning the physiological conditions which modify the secretion of milk. When lactation is fully established, the quantity and quality of the milk secreted become adapted to the requirements of the child at different periods of its existence. In studying the composition of the milk, therefore, it will be found to vary considerably in the different stages of lactation. It is evident that, as the development of the child advances, a constant increase of nourishment is demanded; and, as a rule, the mother is capable of supplying all the nutritive requirements of the infant for from eight to twenty months.

During the time when such an amount of nutritive matter is furnished to the child, the quantity of food taken by the mother is sensibly increased; but observations have shown that the secretion of milk is not much influenced by the nature of the food. It is necessary that the mother should be supplied with good, nutritious articles; but, as far as solid food is concerned, there seems to be no great difference between a coarse and a delicate alimentation, and the milk of females in the lower walks of life, when the general condition is normal, is fully as good as in women who are able to live luxuriously. It is, indeed, a fact generally recognized by physiologists, that the secretion of milk is little influenced by any special diet, provided the alimentation be sufficient and of the quality ordinarily required by the system and that it contain none of the few articles of food which are known to have a special influence upon lactation. So long as the mother is healthy and well-nourished, the milk will take care of itself; and the appetite is the surest guide to the proper variety, quality, and quantity of food. It is very common, however, for females to become quite fat during lactation; which shows that the fatty elements of the food do not pass exclusively into the milk, but that there is a tendency, at the same time, to a deposition of adipose tissue in the ordinary situations in which it is found. It is a matter of common experience, that certain articles, such as acids and fermentable substances, often disturb the digestive organs of the child without producing any change in the milk, that can be recognized by chemical analysis. The individual differences in women, in this regard, are very great.

The statements with regard to solid food do not apply to liquids. During lactation, there is always an increased demand for water and for liquids generally; and, if these be not supplied in sufficient quantity, the secretion of milk is diminished, and its quality is almost always impaired. It is a curious fact, which has been fully established by observations upon the human subject and the inferior animals, that, while the quantity of milk is increased by taking a large amount of simple water, the solid constituents are also increased, and the milk retains all of its qualities as a nutritive fluid.

Alcohol, especially when largely diluted, as in malt-liquors and other mild beverages, is well known to exert an influence upon the secretion of milk. Drinks of this kind almost always temporarily increase the activity of the secretion, and sometimes they produce a certain amount of effect upon the child; but direct and accurate observations on the actual passage of alcohol into the milk are wanting. During lactation, the moderate use of drinks containing a small proportion of alcohol is frequently beneficial, particularly in assisting the mother to sustain the unusual drain upon the system. There are, however, few instances of normal lactation in which their use is absolutely necessary.

It is well known that the secretion of milk may be profoundly affected by violent mental emotions. This is the case in many other secretions, as the saliva and the gastric juice. It is hardly necessary, however, to cite the numerous instances of modification or arrest of the secretion from this cause, which are quoted in many works. Vernois and Becquerel mention a very striking case, in which a hospital wet-nurse, who had lost her only child from pneumonia, became violently affected with grief and presented, as a consequence, an immediate diminution in the quantity of her milk, with a great reduction in the proportion of salts, sugar, and butter. In this case the proportion of caseine was increased. Sir Astley Cooper mentions two cases in which the secretion of milk was instantaneously and permanently arrested from terror. These cases are types of numerous others, which have been reported by writers, of the effects of mental emotions upon secretion.

In the present state of our knowledge, we can comprehend the influence of mental emotions upon secretion, only by assuming that they operate through the nervous system; and, in many of the glands, the influence of the nerves has been clearly demonstrated by actual experiment. Direct observations, however, upon the influence of the nerves upon the mammary glands are few and unsatisfactory. The operation of dividing the nerves distributed to these glands, which has occasionally been practised upon animals in lactation, has not been observed to produce any sensible diminution in the quantity of the secretion. It is difficult, however, to operate upon all the nerves distributed to these organs.

Quantity of Milk.—It is very difficult to form a reliable estimate of the average quantity of milk secreted by the human female in the twenty-four hours. The amount undoubtedly varies very much in different persons; some women being able to nourish two children, while others, though apparently in perfect health, furnish hardly enough food for one. Cooper, as the result of direct observation, states that the quantity that can be drawn from a full breast is usually about two fluidounces. This may be assumed to be about the quantity contained in the lactiferous ducts when they are moderately distended. Lehmann, taking for the basis of his calculations the observations of Lampérierre, who found, as the result of sixty-seven experiments, that from fifty to sixty grammes of milk were secreted in two hours, estimates that the average quantity discharged in twenty-four hours is 1,320 grammes, or about 44·5 fluidounces. Taking into consideration the evident variations in the quantity of milk secreted by different women, it may be assumed that the daily production is from two to three pints.

Certain conditions of the female are capable of materially influencing the quantity of milk secreted. It is evident that the secretion is usually somewhat increased within the first few months of lactation, when the progressive development of the child demands an increase in the quantity of nourishment. If the menstrual function become reëstablished during lactation, the milk is usually diminished in quantity during the periods, but sometimes it is not affected, either in its quantity or composition. Should the female become pregnant, there is generally a great diminution in the quantity of milk, and that which it secreted is ordinarily regarded as possessing little nutritive power. In obedience to a popular prejudice, apparently well-founded, the child is usually taken from the breast as soon as pregnancy is recognized. Authors have not noted any marked and constant variations in the quantity of milk in females of different ages.

Properties and Composition of the Milk.

The general appearance and characters of ordinary cow's milk are sufficiently familiar and may serve as a standard for comparison with the milk of the human female. Human milk is neither so white nor so opaque as cow's milk, having ordinarily a slightly bluish tinge. The milk of different healthy women presents some variation in this regard. After the secretion has become fully established, the fluid possesses no visicidty and is nearly opaque. It is almost inodorous, of a peculiar soft and sweetish taste, and, when perfectly fresh, has a decidedly alkaline reaction. The taste of human milk is sweeter than that of cow's milk. A short time after its discharge from the gland, the reaction of milk becomes faintly acid; but this change takes place more slowly in human milk than in the milk of most of the inferior animals.

The average specific gravity of human milk, according to Vernois and Becquerel, is 1032; although this is subject to considerable variation, the minimum of eighty-nine observations being 1025, and the maximum, 1046. The observations of most physiological chemists have shown that this average is nearly correct.

Milk is not coagulated by heat, even after prolonged boiling; but a thin pellicle then forms on the surface, which is probably due to the combined action of heat and the atmosphere upon the caseine. Although a small quantity of albumen exists in the milk, this does not coagulate on the surface by the action of the heat, for the scum does not form when the fluid is heated in an atmosphere of carbonic acid or of hydrogen, or in a vacuum.

When the milk is coagulated by any substance acting upon the caseine, or when it coagulates spontaneously, it separates into a curd, composed of caseine with most of the fatty particles, and a nearly clear, greenish-yellow serum, called whey. This separation occurs spontaneously, at a variable time after the discharge of the milk, taking place much more rapidly in warm than in cold weather. It is a curious fact that fresh milk is frequently coagulated during a thunder-storm, a phenomenon which has never been satisfactorily explained.

On being allowed to stand for a short time, the milk separates, without coagulating, into two tolerably distinct portions. A large proportion of the globules rises to the top, forming a yellowish-white and very opaque fluid, called cream, leaving the lower portion poorer in globules and of a decidedly bluish tint. In healthy milk, the stratum of cream forms from one-fifth to one-third of the entire mass of the milk. In the human subject, the skim-milk is not white and opaque, but it is nearly as transparent as the whey. A very good method of testing the richness of milk is by the use of little graduated glasses, called lactometers, by which we can measure the thickness of the layer of cream. The specific gravity of the cream from milk of the average specific gravity of 1032 is about 1024. The specific gravity of skim-milk is about 1034.

Microscopical Characters of the Milk.—If a drop of milk be examined with a magnifying power of from three hundred to six hundred diameters, the cause of its opacity will be apparent. It contains an immense number of minute globules, of great refractive power, held in suspension in a clear fluid. These are known under the name of milk-globules and are composed of margarine, oleine, and a fatty matter, peculiar to milk, called butyrine. In human milk the particles are perfectly spherical; but in cow's milk they are often polyhedric from mutual compression. This difference is due to the softer consistence of the butter in human milk, the globules containing a much larger proportion of oleine; and, if cow's milk be warmed, the particles also assume a spherical form.

The human milk-globules measure from $\frac{1}{25000}$ to $\frac{1}{1250}$ of an inch in diameter. They are usually distinct from each other, but they may occasionally become collected into groups without indicating any thing abnormal. In a perfectly normal condition of the glands, when the lacteal secretion has become fully established, the milk contains nothing but a clear fluid with these globules in suspension. The proportion of fatty matter in the milk is from twenty-five to forty-eight parts per thousand, and this gives an idea of the proportion of globules which are seen on microscopical examination.

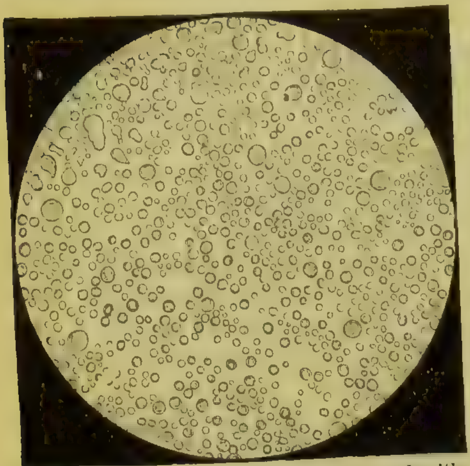


FIG. 103.—*Human milk-globules, from a healthy lying-in woman, eight days after delivery.* (Funke.)

There has been a great deal of discussion with regard to the anatomical constitution of the milk-globules. In many late works it is stated that these are true anatomical elements, composed of fatty matters surrounded by an albuminoid membrane; but some writers assume that the fat is merely in the form of an emulsion and is simply divided into globules and held in suspension, like the fatty particles of the chyle. No one, however, has assumed to have seen the investing membrane of the milk-globules, and its existence is only inferred from the behavior of these little particles in the presence of certain reagents. It is unnecessary to review in detail the numerous opinions that have been advanced on this subject. As far as can be ascertained by simple examination, even with the highest magnifying powers, the globules appear perfectly homogeneous; and the burden of proof rests with those who profess to be able to demonstrate the existence of an investing membrane. Robin, one of the highest authorities on these subjects, argues against the existence of a membrane and opposes the observations of those who assume to have demonstrated it, by explanations of the phenomena produced by reagents, which do not involve, as a necessity, the presence of such a structure. The arguments in favor of its existence are not very satisfactory; and the experiments upon which they are based relate chiefly to the action of ether upon the globules before and after the action of other reagents.

If a quantity of milk be shaken up with an equal volume of ether, the mixture remains opaque; but, if a little potash be added, the fatty matters are dissolved, and the mixture then becomes more or less clear. These facts are all that can be observed without following out the changes with the microscope. Robin has shown that the fatty particles are acted upon when the milk is thoroughly agitated with ether alone; and that the opacity is then due to the fact that the ether, with the fat in solution, is itself in the form of an emulsion. If the opaque mixture of milk and ether be examined with the microscope, globules are seen, larger than the ordinary milk-globules, paler, and possessing much less refractive power. These he supposes to be composed of fat and ether. If potash be added, either before or after the addition of ether, the constitution of the whole mass of liquid is changed, and it becomes somewhat transparent, though by no means perfectly clear. It is assumed that, in the first instance, the ether does not attack the globules, because it has no effect upon the membrane which is supposed to exist, and that the potash acts upon the membrane, allowing the ether then to take up the fat; but, if the observations of Robin be correct, it is evident that this view cannot be sustained.

If dilute acetic acid be added to a specimen of milk under the microscope, the globules become deformed, and some of them show a tendency to run together; an appearance which is supposed by Henle, who was the first to study closely the action of acetic acid upon the milk-globules, to indicate the existence of a membrane. This deduction, however, is not justifiable. Acetic acid readily coagulates the caseine, a principle which is most efficient in maintaining the fat in its peculiar condition. The coagulating caseine then presses upon the globules, and produces, in this way, all the changes in form that have been observed.

Most of the other arguments in favor of the existence of a membrane have no support from direct observation, and consequently they do not demand special consideration; while all the facts which we have been able to find relating to this subject go to show that the fatty matters in the milk are in the condition of a simple emulsion. The precise condition, however, of the fluid immediately surrounding the globules is not fully understood. Certain of the constituents of fluids capable of forming emulsive mixtures with liquid fats may form a coating of excessive tenuity immediately around the globules, but they never constitute distinct membranes capable of resisting the action of solvents upon the fats; and, in the case of the milk, they do not prevent the mechanical union of the globules into masses, as occurs in the process of churning. Milk-globules less than $\frac{1}{5000}$ of an inch in diameter present under the microscope that peculiar oscillating motion known as the Brownian movement. This is arrested on the addition of acetic acid, by coagulation of the caseine. From these facts, it is evident that the milk-globules are composed simply of fat in the form of a fine emulsion. They are not true anatomical elements, originating by a process of genesis in a blastema, undergoing physiological decay, and capable of self-regeneration from materials furnished by the menstruum in which they are suspended, like the blood-corpuscles or leucocytes. They are simply elements of secretion.

Composition of the Milk.—We do not propose, in treating of the composition of the milk, to consider the various methods of analysis which have been employed by different chemists. The only constituent that has ever presented much difficulty in the estimation of its quantity is caseine; but the various processes now employed for its extraction have led to nearly identical results. The following table, compiled by Robin from the analyses of various chemists, gives the constituents of human milk:

Composition of Human Milk.

Water			
Caseine (desiccated)	902·717	to	863·149
Lacto-proteine	29·000	"	39·000
Albumen	1·000	"	2·770
Butter, 25 to 38 { Margarine	traces	"	0·880
Butter, 25 to 38 { Oleine	17·000	"	25·840
Butter, 25 to 38 { Butyrine, caprine, caproïne, capriline	7·500	"	11·400
Sugar of milk (lactine, or lactose)	0·500	"	0·760
Lactate of soda (?)	37·000	"	49·000
Chloride of sodium	0·420	"	0·450
Chloride of potassium	0·240	"	0·340
Carbonate of soda	1·440	"	1·830
Carbonate of lime	0·053	"	0·056
Phosphate of lime of the bones	0·069	"	0·070
Phosphate of magnesia	2·310	"	3·440
Phosphate of soda	0·420	"	0·640
Phosphate of iron (?)	0·225	"	0·230
Sulphate of soda	0·032	"	0·070
Sulphate of potassa	0·074	"	0·075
			traces.
	1,000·000		1,000·000

Gases in solution { Oxygen...... 1·29; Nitrogen..... 12·17; Carbonic acid. 16·54 } 30 parts per 1,000 in volume. (Hoppe.)

The proportion of water in milk is subject to a certain amount of variation, but this is not so considerable as might be expected from the great variations in the entire quantity of the secretion. In treating of the quantity of milk in the twenty-four hours, we have seen that the influence of drinks, even when nothing but pure water has been taken, is very marked; and, although the activity of the secretion is much increased by fluid ingesta, the quality of the milk is not usually affected, and the proportion of water to the solid matters remains about the same.

Nitrogenized Constituents of Milk.—Very little remains to be said concerning the nitrogenized constituents of human milk, after what has been stated under the head of alimentation. The different principles of this class undoubtedly have the same nutritive function and they appear to be identical in all varieties of milk, the only difference being in their relative proportion. It is a matter of common experience, indeed, that the milk of many of the lower animals will take the place of human milk, when prepared so as to make the proportions of its different constituents approximate the composition of the natural food of the child. A comparison of the composition of human milk and cow's milk shows that the former is poorer in nitrogenized matters and richer in butter and sugar; and consequently, the upper strata of cow's milk, appropriately sweetened and diluted with water, very nearly represent the ordinary breast-milk.

Caseine is by far the most important of the nitrogenized principles of milk, and it supplies nearly all of this kind of nutritive matter demanded by the child. Lacto-proteine, a principle described by Millon and Commaille, is not so well defined, and albumen exists in the milk in very small quantity. That albumen always exists in milk, can readily be shown by the following process described by Bernard: If milk, treated with an excess of sulphate of magnesia so as to form a thin paste, be thrown upon a filter, the caseine and fatty matters will be retained, and the clear liquid that passes through shows a marked opacity upon the application of heat or the addition of nitric acid.

The coagulation of milk depends upon the reduction of caseine from a liquid to a semisolid condition. When milk is allowed to coagulate spontaneously, or sour, the change is effected by the action of the lactic acid which results from a transformation of a portion of the sugar of milk. Caseine, in fact, is coagulated by any of the acids, even the feeble acids of organic origin. It differs from albumen in this regard and in the fact that it is not coagulated by heat. It has been suggested that, in fresh milk, the caseine exists in combination with carbonate of soda, and that coagulation always takes place from the action of acids upon this salt, by which the caseine is set free. It is true that coagulated caseine may be readily dissolved in a solution of carbonate of soda, but it has been shown that coagulation may be induced by the agency of certain neutral principles, while the milk retains its alkaline reaction. If fresh milk be slightly raised in temperature and be treated with an infusion of the gastric mucous membrane of the calf, coagulation will take place in from five to ten minutes, the clear liquid still retaining its alkaline reaction. Simon has observed that the mucous membrane of the stomach of an infant a few days old, that had recently died, coagulated woman's milk more readily than the mucous membrane of the stomach of the calf.

Non-Nitrogenized Constituents of Milk.—Non-nitrogenized matters exist in abundance in the milk. The liquid caseine and the water hold the fats, as we have seen, in the condition of a fine and permanent emulsion. This fat has been separated from the milk and analyzed by chemists and is known under the name of butter. In human milk, the butter is much softer than in the milk of many of the inferior animals, particularly the cow; but it is composed of essentially the same constituents, although in different proportions. In different animals, there are developed, even after the discharge of the milk, certain odorous principles, which are more or less characteristic of the animal from which the butter is taken.

The greatest part of the butter consists of margarine. It contains, in addition, oleine, with a small quantity of peculiar fats, which have not been very well determined, called butyrine, caprine, caproïne, and capriline. The margarine and oleine are principles found in the fat throughout the body; but the last-named substances are peculiar to the milk. These are especially liable to acidification, and the acids resulting from their decomposition give the peculiar odor and flavor to rancid butter.

Sugar of milk, sometimes called lactine, or lactose, is the most abundant of the solid constituents of the mammary secretion. It is this principle that gives to the milk its peculiar sweetish taste, although this variety of sugar is much less sweet than cane-sugar. The chief peculiarities of milk-sugar are that it readily undergoes change into lactic acid in the presence of nitrogenized ferments and takes on alcoholic fermentation slowly and with difficulty. At one time, indeed, it was supposed that milk-sugar could not be decomposed into alcohol and carbonic acid; but it is now well established that this change can be induced, the only peculiarity being that it takes place very slowly. In some parts of the world, intoxicating drinks are made by the alcoholic fermentation of milk.

A consideration of the nutritive action of the fatty and saccharine constituents of milk belongs properly to the subjects of alimentation and nutrition. It may be stated here, however, that these principles seem to be as necessary to the nutrition of the child as the nitrogenized principles; although the precise manner in which they affect the development and regeneration of the tissues has not been ascertained.

Inorganic Constituents of Milk.—It is probable that many inorganic principles exist in the milk which are not given in the table; and the separation of these principles from their combinations with organic matters is one of the most difficult problems in physiological chemistry. This must be the case for, during the first months of extra-uterine existence, the child derives all the inorganic, as well as the organic matters necessary to nutrition and development, from the breast of the mother. The reaction of the milk depends upon the presence of the alkaline carbonates, and these principles are important in preserving the fluidity of the caseine. It is not determined precisely in what form iron exists in the milk, but its presence here is undoubted. A comparison of the composition of the milk with that of the blood shows that most of the important inorganic principles found in the latter fluid exist also in the milk.

Hoppe has indicated the presence of carbonic acid, nitrogen, and oxygen, in solution in milk. Of these gases, carbonic acid is the most abundant. It is well known that the presence of gases in solution in liquids renders them more agreeable to the taste, and carbonic acid increases very materially their solvent properties. Aside from these considerations, the precise function of the gaseous constituents of the milk is not apparent.

A study of the composition of the milk fully confirms the fact, which we have already had occasion to state, that this is a typical alimentary fluid and presents in itself the proper proportion and variety of material for the nourishment of the body during the period when the development of the system is going on with its maximum of activity. The form in which its different nutritive constituents exist is such that they are easily digested and are assimilated with great rapidity.

Variations in the Composition of the Milk.

Vernois and Becquerel have indicated a certain amount of variation at different ages and at different periods in lactation, but they show, at the same time, that the fluid is not subject to changes in its composition sufficiently great to influence materially the nutrition of the child.

If the composition of the milk be compared at different periods of lactation, it will be found to undergo great changes during the first few days. In fact, the first fluid secreted after parturition is so different from ordinary milk, that it has been called by another name. It is then known as colostrum, the peculiar properties of which will be considered more fully hereafter, under a distinct head. As the secretion of milk becomes established, the fluid, from the first to the fifteenth day, becomes gradually diminished in density and in its proportion of water and of sugar, while there is a progressive increase in the proportion of most of the other constituents, viz., butter, caseine, and the inorganic salts. The milk, therefore, as far as we can judge from its composition, as it increases in quantity during the first few days of lactation, is constantly increasing in its nutritive properties.

The differences in the composition of the milk, taken from month to month during the entire period of lactation, are not so distinctly marked. It is difficult, indeed, to indicate any constant variations of sufficient importance to lead to the view that the milk varies much in its nutritive properties at different times, during the ordinary period of lactation. The differences noted between the milk of primiparæ and multiparæ were very slight and unimportant. As a rule, however, the milk of primiparæ approaches more nearly the normal standard.

The menstrual periods, when they occur during lactation, have been found by most observers to modify considerably the composition and properties of the milk; and it is well known to practical physicians that the secretion is then liable to produce serious disturbances of the digestive system of the child, although frequently these effects are not observed. The changes in the composition of the milk which commonly occur during menstruation are, great increase in the quantity of caseine, increase in the proportion of butter and the inorganic salts, and a slight diminution in the proportion of sugar. The common impression that the milk is unfit for the nourishment of the child if pregnancy occur during lactation is undoubtedly well-founded, although analyses of the milk of pregnant women have never been made upon an extended scale.

In normal lactation, there is no marked and constant difference in composition between milk that has been secreted in great abundance and milk which is produced in comparatively small quantity; nor do we observe that difference between the milk first drawn from the breast and that taken when the ducts are nearly empty, which is observed in the milk of the cow.

The influence of alimentation and the taking of liquids upon lactation relates chiefly to the quantity of milk and has already been considered.

In treating of the influences which modify the secretion of milk, we have already alluded to the effects of violent mental emotions upon the production and the composition of this fluid. The very remarkable case of profound alteration of the milk by violent grief, detailed by Vernois and Becquerel, is the only one in which the secretion in this condition has been carefully analyzed. The changes thus produced in its composition have already been referred to, the most marked difference being observed in the proportion of butter, which became reduced from 23·79 to 5·14 parts per 1,000.

Colostrum.

Near the end of utero-gestation, during a period which varies considerably in different women and has not been accurately determined, a small quantity of a thickish, stringy fluid may frequently be drawn from the mammary glands. This bears little resemblance to perfectly-formed milk. It is small in quantity and is usually more abundant in multiparæ than in primiparæ. This fluid, with that secreted for the first few days after delivery, is called colostrum. It is yellowish, semiopaque, of a distinctly alkaline reaction, and is somewhat mucilaginous in its consistence. Its specific gravity is considerably above that of the ordinary milk, being from 1040 to 1060. As lactation progresses, the character of the secretion rapidly changes, until it becomes loaded with true milk-globules and assumes the characters of ordinary milk.

The opacity of the colostrum is due to the presence of a number of different corpuscular elements. Milk-globules, very variable in size and number, are to be found in the secretion from the first. These, however, do not exist in sufficient quantity to render the fluid very opaque, and they are frequently aggregated in rounded and irregular masses, held together, apparently, by some glutinous matter. Peculiar corpuscles, first accurately described by Donné, under the name of "granular bodies," and supposed to be characteristic of the colostrum, always exist in this fluid. These are now known as colostrum-corpuscles. They are spherical, varying in size from $\frac{1}{2500}$ to $\frac{1}{500}$ of an inch, are sometimes pale, but more frequently quite granular, and they contain very often a large number of fatty particles. They behave in all respects like leucocytes and are described by Robin as a variety of these bodies. Many of them are precisely like the leucocytes found in the blood, lymph, or pus. We now know, however, that the so-called mucus-corpuscle does not differ from the pus-corpuscle or the white corpuscle of the blood; and leucocytes generally, when confined in liquids that are not subject to movements, are apt to undergo enlargement, to become fatty, and, in short, they may present all the different appearances observed in the colostrum-corpuscles. In addition to these corpuscular elements, a small quantity of mucosine may frequently be observed in the colostrum on microscopical examination.

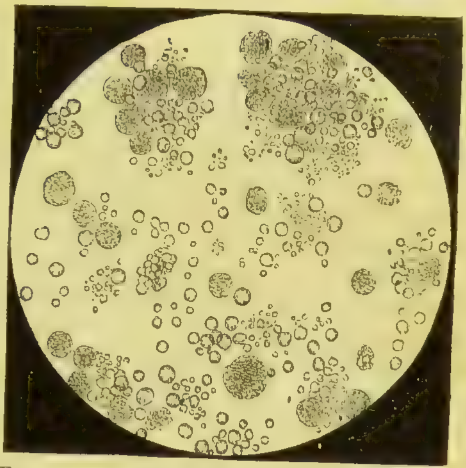


FIG. 104.—*Colostrum, from a healthy lying-in woman, twelve hours after delivery.* (Funke.) The smaller globules are globules of milk; the larger globules, *a*, *a*, filled with granulations, are colostrum-corpuscles. As lactation advances, the colostrum-corpuscles gradually disappear, and the milk-globules become more numerous, smaller, and more uniform in size.

On the addition of ether to a specimen of colostrum under the microscope, most of the fatty particles, both within and without the colostrum-corpuscles, are dissolved. Ammonia added to the fluid renders it stringy, and sometimes the entire mass assumes a gelatinous consistence.

In its proximate composition, colostrum presents many points of difference from true milk. It is sweeter to the taste and contains a greater proportion of sugar and of the inorganic salts. The proportion of fat is at least equal to the proportion in the milk and is generally greater. Instead of caseine, pure colostrum contains a large proportion of albumen; and, as the character of the secretion changes in the process of lactation, the albumen becomes gradually reduced in quantity and caseine takes its place.

The following, deduced from the analyses of Clemm, may be taken as the ordinary composition of colostrum of the human female:

Composition of Colostrum.

Water	945·24
Albumen, and salts insoluble in alcohol	29·81
Butter	7·07
Sugar of milk, extractive matter, and salts soluble in alcohol	17·27
Loss	0·61
	1,000·00

Colostrum ordinarily decomposes much more readily than milk and takes on putrefactive changes very rapidly. If it be allowed to stand for from twelve to twenty-four hours, it separates into a thick, opaque, yellowish cream and a serous fluid. In an observation by Sir Astley Cooper, nine measures of colostrum, taken soon after parturition, after twenty-four hours of repose, gave six parts of cream to three of milk.

The peculiar constitution of the colostrum, particularly the presence of an excess of sugar and inorganic salts, renders it somewhat laxative in its effects, and it is supposed to be useful, during the first few days after delivery, in assisting to relieve the infant of the accumulation of meconium.

As the quantity of colostrum that may be pressed from the mammary glands during the latter periods of utero-gestation, particularly the last month, is very variable, it becomes an interesting and important question to determine whether this secretion have any relation to the quantity of milk that may be expected after delivery. This has been made the subject of careful study by Donné, who arrived at the following important conclusions:

In women in whom the secretion of colostrum is almost absent, the fluid being in exceedingly small quantity, viscid, and containing hardly any corpuscular elements, there is hardly any milk produced after delivery.

In women who, before delivery, present a moderate quantity of colostrum, containing very few milk-globules and a number of colostrum-corpuscles, after delivery the milk will be scanty or it may be abundant, but it is always of poor quality.

When the quantity of colostrum produced is considerable, the secretion being quite fluid and rich in corpuscular elements, particularly milk-globules, the milk after delivery is always abundant and of good quality.

From these observations, it would seem that the production of colostrum is an indication of the proper development of the mammary glands; and the early production of fatty granules, which are first formed by the cells lining the secreting vesicles, indicates the probable activity in the secretion of milk after lactation has become fully established.

The secretion of the mammary glands preserves the characters of colostrum until toward the end of the milk-fever, when the colostrum-corpuscles rapidly disappear, and the milk-globules become more numerous, regular, and uniform in size. It may be stated, in general terms, that the secretion of milk becomes fully established and all the characters of the colostrum disappear at from the eighth to the tenth day after delivery. A few colostrum-corpuscles and masses of agglutinated milk-globules may sometimes be discovered after the tenth day, but they are very rare. After the fifteenth day, the milk does not sensibly change in its microscopical or its chemical characters.

Lacteal Secretion in the Newly-Born.

It is a curious fact that in infants of both sexes there is generally a certain amount of secretion from the mammary glands, commencing at birth or from two to three days after, and continuing sometimes for two or three weeks. The quantity of fluid that may be pressed out at the nipples at this time is very variable. Sometimes only a few drops can be obtained, but occasionally the fluid amounts to one or two drachms. Although it is impossible to indicate the object of this secretion, which takes place when the glands are in a rudimentary condition, it has been so often observed and described by physiologists, that there can be no doubt with regard to the nature of the fluid and the fact that the secretion is almost always produced in greater or less quantity. The following is an analysis by Quevenne of the secretion obtained by Gubler. The observations of Gubler were very extended and were made upon about twelve hundred children. The secretion rarely continued for more than four weeks, but in four instances it persisted for two months.

Composition of the Milk of the Infant.

Water	894·00
Caseine	26·40
Sugar of milk	62·20
Butter	14·00
Earthy phosphates	1·20
Soluble salts (with a small quantity of insoluble phosphates)	2·20
	1,000·00

This fluid does not differ much in its composition from ordinary milk. The proportion of butter is much less, but the amount of sugar is greater, and the quantity of caseine is nearly the same.

Of the other fluids which are enumerated in the list of secretions, the saliva, gastric juice, pancreatic juice, and the intestinal fluids have already been considered in connection with digestion. The physiology of the lachrymal secretion will be taken up in connection with the eye, and the bile will be treated of fully under the head of excretion.

CHAPTER XII.

EXCRETION BY THE SKIN AND KIDNEYS.

Differences between the secretions proper and the excretions—Physiological anatomy of the skin—Physiological anatomy of the nails and hairs—Sudden blanching of the hair—Uses of the hairs—Perspiration—Sudoriparous glands—Mechanism of the secretion of sweat—Properties and composition of the sweat—Peculiarities of the sweat in certain parts—Physiological anatomy of the kidneys—Distribution of blood-vessels in the kidneys—Lymphatics and nerves of the kidneys—Mechanism of the production and discharge of urine—Formation of the excrementitious constituents of the urine in the tissues, absorption of these principles by the blood, and separation of them from the blood by the kidneys—Effects of removal of both kidneys from a living animal—Effects of tying the ureters in a living animal—Extirpation of one kidney—Influence of blood-pressure, the nervous system, etc., upon the secretion of urine—Alternation in the action of the kidneys upon the two sides—Changes in the composition of the blood in passing through the kidneys—Physiological anatomy of the urinary passages—Mechanism of the discharge of urine—Properties and composition of the urine—General physical properties of the urine—Quantity, specific gravity, and reaction of the urine—Composition of the urine—Gases of the urine—Variations in the composition of the urine—Variations produced by food—Urina potus, urina cibi, and urina sanguinis—Influence of muscular exercise upon the urine—Influence of mental exertion.

In entering upon the study of the elimination of effete matters, it is necessary to appreciate fully the broad distinctions between the secretions proper and the excretions, in their composition, the mechanism of their production, and their destination. These considerations are again referred to, for the reason that they have not ordinarily received that attention in works upon physiology which their importance seems to demand. The mechanism of excretion is inseparably connected with the function of nutrition, and it forms one of the great starting-points in the study of all the modifications of nutrition in diseased conditions.

Taking the urine as the type of the excrementitious fluids, it is found to contain none of those principles included in the class of non-crystallizable, organic nitrogenized matters, but is composed entirely of crystallizable matters, simply held in solution in water. The character of these principles depends upon the constitution of the blood and the general condition of nutrition, and not upon any formative action in the glands. The principles themselves represent the ultimate physiological changes of certain constituent parts of the living organism, and they are in such a condition that they are of no farther use in the economy and are simply discharged from the body. Certain inorganic matters are found in the excrementitious fluids, are discharged with the products of excretion, and are thus associated with the organic principles of the economy in their physiological destruction, as well as in their deposition in the tissues. Coagulable organic matters, or albuminoid principles, never exist in the excrementitious fluids under normal conditions; except as the products of other glands may become accidentally or constantly mixed with the excrementitious fluids proper. The same remark applies to the non-nitrogenized matters (sugars and fats), which, whether formed in the organism or taken as food, are consumed as such in the process of nutrition. The production of the excretions is constant, being subject only to certain modifications in activity, which are dependent upon varying conditions of the system. All of the elements of excretion preëxist in the blood, either in the precise condition in which they are discharged or in some slightly-modified form.

Under the head of excretion, it is proposed to consider the general properties and composition of the different excrementitious fluids; but the relations of the excrementitious matters themselves to the tissues will be more fully treated of in connection with nutrition.

The urine is a purely excrementitious fluid. The perspiration and the secretion of the axillary glands are excrementitious fluids, but they contain a certain amount of the secretion of the sebaceous glands. Certain excrementitious matters are found in the bile, but, at the same time, this fluid contains principles manufactured in the liver and has an important function as a secretion, in connection with the process of digestion.

Physiological Anatomy of the Skin.

The skin is one of the most complex and important structures in the body, and it possesses a variety of functions. In the first place, it forms a protective covering for the general surface. It is quite thick over the parts most subject to pressure and friction, is elastic over movable parts and those liable to variations in size, and, in many situations, is covered with hair, which affords an additional protection to the subjacent structures. The skin and its appendages are imperfect conductors of caloric, are capable of resisting very considerable variations in temperature, and they thus tend to maintain the normal standard of the animal heat. As an organ of tactile sensibility, the skin has an important function, being abundantly supplied with sensitive nerves, some of which present an arrangement peculiarly adapted to the nice appreciation of external impressions. The skin assists in preserving the external forms of the muscles. It also relieves the abrupt projections and depressions of the general surface and gives roundness and grace to the contours of the body. In some parts it is very closely attached to the subjacent structures, while in others it is less adherent and is provided with a layer of adipose tissue.

As an organ of excretion, the skin is very important; and, although the quantity of excrementitious matter exhaled from it is not very great and probably not subject to much variation, the evaporation of water from the general surface is always considerable and is subject to such modifications as may become necessary from the varied conditions of the animal temperature. Thus, while the skin protects the body from external influences, its function is important in regulating the heat produced as one of the numerous phenomena attendant upon the general process of nutrition.

As the skin presents such a variety of functions, its physiological anatomy is most conveniently considered in connection with different divisions of the subject of physiology. For example, under the head of secretion, we have already taken up the structure of the different varieties of sebaceous glands; and the anatomy of the skin as an organ of touch will be most appropriately considered in connection with the nervous system. In this connection, we shall describe the excreting organs found in the skin; and here it will be most convenient to study briefly its general structure and the most important points in the anatomy of the epidermic appendages. A full and connected description of the skin and its appendages belongs properly to works upon anatomy.

Extent and Thickness of the Skin.—Sappey has made a number of very careful observations upon the extent of the surface of the skin. Without detailing the measurements of different parts, it may be stated, as the general result of his observations, that the cutaneous surface in a good-sized man is equal to a little more than sixteen square feet; and, in men of more than ordinary size, it may extend to twenty-one or twenty-two square feet. In women of medium size, as the mean result of three observations, the surface was found to equal about twelve square feet. When we consider the great extent of the cutaneous surface, it is not surprising that the amount of secretion, under certain conditions, should be enormous. Indeed, under all circumstances, the amount of elimination is very considerable, and the skin is really one of the most important of the organs of excretion.

The thickness of the skin varies very much in different parts. Where it is exposed to constant pressure and friction, as on the soles of the feet or the palms of the hands, the epidermis becomes very much thickened, and in this way the more delicate structure of the true skin is protected. It is well known that the development of the epidermis, under these conditions, varies in different persons, with the amount of pressure and friction to which the surface is habitually subjected. The true skin is from $\frac{1}{12}$ to $\frac{1}{8}$ of an inch in thickness; but in certain parts, particularly in the external auditory meatus, the lips, and the glans penis, it frequently measures not more than $\frac{1}{100}$ of an inch.

Layers of the Skin.—The skin is naturally divided into two principal layers, which may be readily separated from each other by maceration. These are, the true skin (cutis vera, derma, or corium), and the epidermis, cuticle, or scarf-skin. The true skin is attached to the subjacent structures, more or less closely, by a fibrous structure called the subcutaneous areolar tissue, in the meshes of which we commonly find a certain quantity of fatty tissue. This layer is sometimes described under the name of the panniculus adiposus. The thickness of the adipose layer varies very much in different parts of the general surface and in different persons. There is no fat beneath the skin of the eyelids, the upper and outer part of the ear, the penis, and the scrotum. Beneath the skin of the cranium, the nose, the neck, the dorsum of the hand and foot, the knee, and the elbow, the fatty layer is about $\frac{1}{12}$ of an inch in thickness. In other parts it usually measures from $\frac{1}{6}$ to $\frac{1}{2}$ of an inch. In very fat persons it may measure one inch or more. Upon the head and the neck, in the human subject, are muscles attached more or less closely to the skin. These are capable of moving the skin to a slight extent. Muscles of this kind are largely developed and quite extensively distributed in some of the lower animals.

There is no sharply-defined line of demarcation between the cutis and the subcutaneous areolar tissue; and the under surface of the skin is always irregular, from the presence of numerous fibres which are necessarily divided in detaching it from the subjacent structures. The fibres which enter into the composition of the skin become looser in their arrangement near its under surface, the change taking place rather abruptly, until they present large aveolæ, which generally contain a certain amount of adipose tissue.

The layer called the true skin is subdivided into a deep, reticulated, or fibrous layer, and a superficial portion, called the papillary layer. The epidermis is also divided into two layers, as follows: an external layer, called the horny layer; and an internal layer, called the Malpighian, or the mucous layer, which is in contact with the papillary layer of the corium.

The Corium, or True Skin.—The reticulated and the papillary layer of the true skin are quite distinct. The lower stratum, the reticulated layer, is much thicker than the papillary layer and is dense, resisting, quite elastic, and slightly contractile. It is composed of numerous bundles of white fibrous tissue interlacing with each other in every direction, generally at acute angles. Distributed throughout this layer, are found numerous anastomosing, elastic fibres of the small variety, and with them a number of non-striated muscular fibres. This portion of the skin contains, in addition, a considerable quantity of amorphous matter, which serves to hold the fibres together. The muscular fibres are particularly abundant about the hair-follicles and the sebaceous glands connected with them, and their arrangement is such that, when they are excited to contraction by cold or by electricity, the follicles are drawn up, projecting upon the general surface and producing the appearance known as "goose-flesh." Contraction of these fibres is particularly marked about the nipple, producing the so-called erection of this organ, and about the scrotum and penis, wrinkling the skin of these parts. The peculiar arrangement of the little muscles around the hair-follicles, forming little bands attached to the surface of the true skin and the base of the follicles, explains fully the manner in which the "goose-flesh" is produced. (See Fig. 107, page 387.) Contraction of the skin, in obedience to the stimulus of electricity, has been repeatedly demonstrated, both in the living subject and in executed criminals immediately after death.

The papillary layer of the skin passes insensibly into the subjacent structure and presents no well-marked line of division. It is composed chiefly of amorphous matter like that which exists in the reticulated layer. The papillæ themselves appear to be simple elevations of this amorphous matter, although they may contain a few fibres. In this layer, we find a number of fibro-plastic nuclei, with a few little corpuscular bodies called by Robin, cytoblastions.

As regards their form, the papillæ may be divided into two varieties; the simple and the compound. The simple papillæ are conical, rounded, or club-shaped elevations of the amorphous matter and are irregularly distributed on the general surface. The smallest are from $\frac{1}{700}$ to $\frac{1}{400}$ of an inch in length and are found chiefly upon the face. The largest are on the palms of the hands, the soles of the feet, and the nipple. These measure from $\frac{1}{250}$ to $\frac{1}{200}$ of an inch. Large papillæ, regularly arranged in a longitudinal direction, are found beneath the nails. The regular, curved lines observed upon the palms of the hands and the soles of the feet, particularly the palmar surfaces of the last phalanges, are formed by double rows of compound papillæ, which present two, three, or four points attached to a single base. In the centre of each of these double rows of papillæ, is an excessively fine and shallow groove, in which are found the orifices of the sudoriferous ducts.

The papillæ are abundantly supplied with blood-vessels, terminating in looped capillary plexuses, and with nerves. The termination of the nerves is peculiar and will be fully described in connection with the organs of touch. The arrangement of the lymphatics, which are very numerous in the skin, has already been indicated in the general description of the lymphatic system.

The Epidermis and its Appendages.—The epidermis, or external layer of the skin, is a membrane composed exclusively of cells, containing neither blood-vessels, nerves, nor lymphatics. Its external surface is marked by exceedingly shallow grooves, which correspond to the deep furrows between the papillæ of the derma. Its internal surface is applied directly to the papillary layer of the true skin and follows closely all its inequalities. This portion of the skin is subdivided into two tolerably-distinct layers. The internal layer is called the rete mucosum, or the Malpighian layer, and the external is called the horny layer. These two layers present certain important distinctive characters.

The Malpighian layer is composed of a single stratum of prismoidal, nucleated cells, containing a greater or less amount of pigmentary matter, which are applied directly to all the inequalities of the derma, and of a number of layers of rounded cells containing no pigment. The upper layers of cells, with the scales of the horny layer, are semitransparent and nearly colorless; and it is the pigmentary layer chiefly which gives to the skin its characteristic color and the peculiarities in the complexion of different races and of different individuals. In the negro, this layer is nearly black; and, when the epidermis is removed, the true skin does not present any marked difference from the skin of the white race. All the epidermic cells are somewhat colored in the dark races, but the upper layers contain no pigmentary granules. The cells of the pigmentary layer are from $\frac{1}{4000}$ to $\frac{1}{2000}$ of an inch in length and from $\frac{1}{5000}$ to $\frac{1}{4000}$ of an inch in their short diameter. The rounded cells in the upper layers are from $\frac{1}{4000}$ to $\frac{1}{3000}$ of an inch in diameter. The absolute thickness of the rete mucosum is from $\frac{1}{1700}$ to $\frac{1}{75}$ of an inch.

The horny layer is composed of numerous strata of hard, flattened cells, irregularly polygonal in shape, generally without nuclei, and measuring from $\frac{1}{2000}$ to $\frac{1}{750}$ of an inch in diameter. The deeper cells are thicker and more rounded than those of the superficial layers.

The epidermis serves as a protection to the more delicate structure of the true skin, and its thickness is proportionate to the exposure of the different parts. It is consequently much thicker upon the soles of the feet and the palms of the hands than in other portions of the general surface, and its thickness is very much increased in those who are habitually engaged in manual labor. Upon the face, the eyelids, and in the external auditory passages, the epidermis is most delicate, measuring from $\frac{1}{300}$ to $\frac{1}{600}$ of an inch in thickness. Upon the palm it is from $\frac{1}{36}$ to $\frac{1}{24}$ of an inch thick, and upon the sole of the foot it measures from $\frac{1}{16}$ to $\frac{1}{9}$ of an inch. These variations in thickness depend entirely upon the development of the horny layer. The thickness of the rete mucosum, although it presents considerable variation in different parts, is rather more uniform.

There is constantly more or less desquamation of the epidermis, particularly of the horny layer, and the cells are regenerated by a blastema exuded from the subjacent vascular parts. It is probable that there is a constant formation of cells in the deeper strata of the horny layer, which become flattened as they near the surface; but there is no direct evidence that the cells of the rete mucosum undergo transformation into the hard, flattened scales of the horny layer.

Physiological Anatomy of the Nails and Hairs.—It is unnecessary, in this connection, to discuss very minutely the anatomy of the nails and hairs. They are ordinarily regarded as appendages of the epidermis, produced by certain peculiar organs belonging to the true skin; and an elaborate study of these parts belongs strictly to descriptive and general anatomy. To complete, however, the physiological history of the skin, it will be necessary to consider briefly the general arrangement of the cuticular appendages.

The nails are situated on the dorsal surfaces of the distal phalanges of the fingers and toes. They serve to protect these parts, and, in the fingers, they are quite important in prehension. The general appearance of the nails is so familiar that it requires no special description. In their study, anatomists have distinguished a root, a body, and a free border.

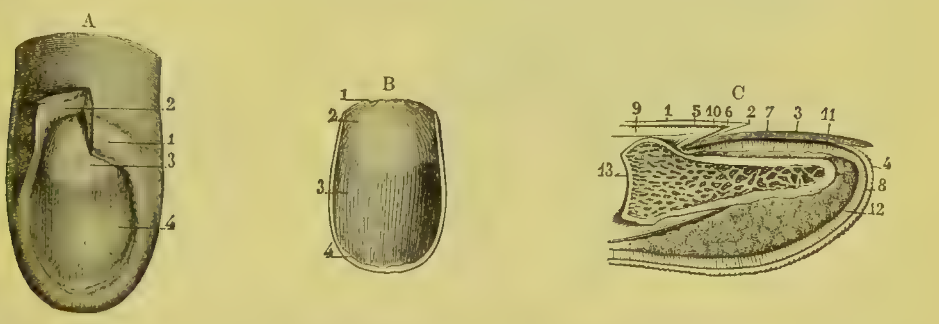


FIG. 105.—*Anatomy of the nails.* (Sappey.)

A, nail *in situ*: 1, cutaneous fold covering the root of the nail; 2, section of this fold, turned back to show the root of the nail; 3, lunula; 4, nail. B, concave or adherent surface of the nail: 1, border of the root; 2, lunula and root; 3, body; 4, free border. C, longitudinal section of the nail: 1, 2, epidermis; 3, superficial layer of the pulp of the finger; 4, epidermis of the pulp of the finger; 5, 6, true skin; 7, 11, bed of the nail; 8, Malpighian layer of the nail; 9, 10, true skin on the dorsal surface of the finger; 12, true skin of the pulp of the finger; 13, last phalanx of the finger.

The root of the nail is thin and soft, terminating in rather a jagged edge, which is turned slightly upward and is received into a fold of the skin extending around the nail to its free edge. The length of the root of course varies with the size of the nail, but it is generally from one-fourth to one-third of the length of the body.

The body of the nail extends from the fold of skin which covers the root to the free border. This portion of the nail, with the root, is closely adherent by its under surface to the true skin. It is marked by fine but distinct longitudinal striæ and very faint transverse lines. It is usually reddish in color, from the great vascularity of the subjacent structure. At the posterior part, is a whitish portion of a semilunar shape, called the lunula, which has this appearance simply from the fact that the corium in this part is less vascular and the papillæ are not so regular as in the rest of the body. That portion of the skin situated beneath the root and the body of the nail is called the matrix. It presents highly vascular papillæ, arranged in regular, longitudinal rows, and it receives into its grooves corresponding ridges on the under surface of the nail.

The free border of the nail begins at the point where the nail becomes detached from the skin. This is generally cut or worn away and is constantly growing; but, if left to itself, it attains in time a definite length, which may be stated, in general terms, to be from an inch and a half to two inches.

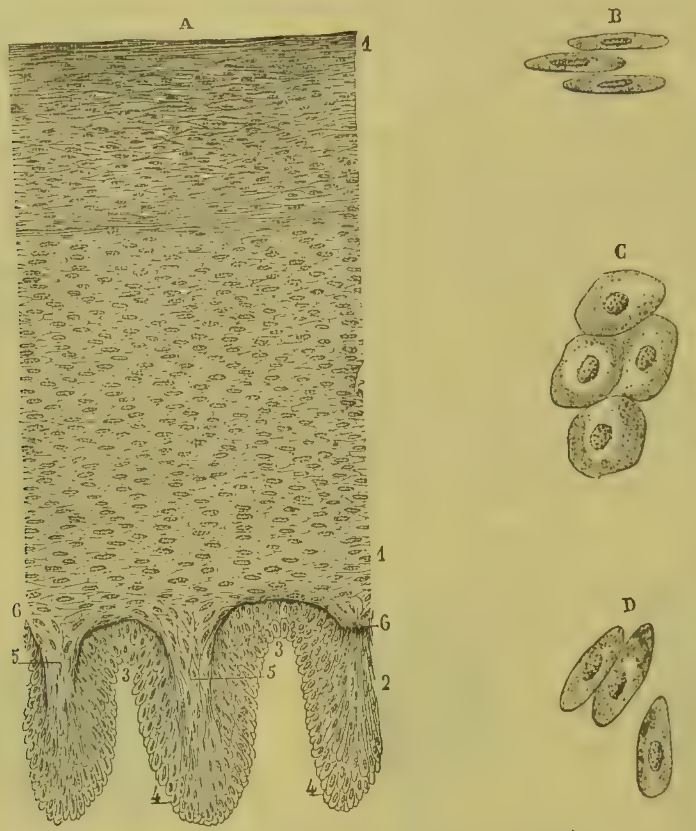


FIG. 106.—*Section of the nail, etc.* (Sappey.)
A, section of the nail: 1, 1, superficial layer; 2, deep layer; 3, 3, 4, 4, section of the grooves on the attached surface; 5, 5, union of the superficial with the deep layer; 6, 6, dark line between the two layers. B, cells of the superficial layer, lateral view. C, cells of the superficial layer, flat view. D, cells of the deep layer.

Examining the nail in a longitudinal section, the horny layer, which is usually regarded as the true nail, is found to increase progressively in thickness from the root to near the free border. If the nail be examined in a transverse section, it will also be found much thicker in the central portion than near the edge, and that part which is received into the lateral portions of the fold becomes excessively thin like the rest of the root. The thickness of the true nail at the root is from $\frac{1}{200}$ to $\frac{1}{150}$ of an inch; and, in the thickest portion of the body, it usually measures from $\frac{1}{40}$ to $\frac{1}{30}$ of an inch. The nail becomes somewhat thinner at and near the free border.

Sections of the nails show that they are composed of two layers, which correspond to the Malpighian and the horny layer of the epidermis, although they are much more distinct. The Malpighian layer is applied directly to the ridges of the bed of the nail and presents upon its upper surface ridges much less strongly marked than those of the underlying true skin. This layer is rather thinner than the horny layer, is whitish in color, and is composed of numerous strata of elongated, prismoidal, nucleated cells, arranged perpendicularly to the matrix. These cells are from $\frac{1}{3000}$ to $\frac{1}{1700}$ of an inch in length.

The horny layer, which constitutes the true nail, is applied by its under surface directly to the ridges of the Malpighian layer. It is dense and brittle and is composed of numerous strata of flattened cells, which cannot be isolated without the use of reagents. If the different strata of this portion of the nail be studied after boiling in a dilute solution of soda or potash, it becomes evident that here, as in the horny layer of the epidermis, the lower cells are somewhat rounded, while those nearer the surface are flattened. These cells are nearly all nucleated and measure from $\frac{1}{1000}$ to $\frac{1}{750}$ of an inch in diameter. The thickness of this layer varies in different portions of the nail, while that of the Malpighian layer is nearly uniform. This layer is constantly growing, and it constitutes the entire substance of the free borders of the nails.

The connections of the nails with the true skin resemble those of the epidermis; but the relations of these structures to the epidermis itself are somewhat peculiar. Up to the fourth month of fœtal life, the epidermis covering the dorsal surfaces of the last phalanges of the fingers and toes does not present any marked peculiarities; but, at about the fourth month, the peculiar hard cells of the horny layer of the nails make their appearance between the Malpighian and the horny layer of the epidermis, and at the same time the Malpighian layer beneath this plate, which is destined to become the Malpighian layer of the nails, is somewhat thickened, and the cells assume more of an elongated form. The horny layer of the nails constantly thickens from this time; but, until the end of the fifth month, it is covered by the horny layer of the epidermis. After the fifth month, the epidermis breaks away and disappears from the surface; and, at the seventh month, the nails begin to increase in length. Thus, at one time, the nails are actually included between the two layers of the epidermis; but, after they have become developed, they are simply covered at their roots by a narrow border of the horny layer, the epidermis commencing again under the nail where the free border leaves the bed. The nails are therefore to be regarded as modifications of the horny layer of the epidermis, possessing certain anatomical and chemical peculiarities. The Malpighian layer of the nails is continuous with the same layer of the epidermis, but the horny layers are, as we have seen, distinct.

One of the most striking peculiarities of the nails is in their mode of growth. The Malpighian layer is stationary, but the horny layer is constantly growing, if the nails be cut, from the root and bed. It is evident that the nails grow from the bed, as their thickness progressively increases in the body from the root to near the free border; but their longitudinal growth is by far the more rapid. Indeed, the nails are constantly pushing forward, increasing in thickness as they advance. Near the end of the body of the nail, as the horny layer becomes thinner, the growth from below is diminished.

Hairs, varying greatly in size and development, cover nearly every portion of the cutaneous surface. The only parts in which they are not found are the palms of the hands and soles of the feet, the palmar surface of the fingers and toes, the dorsal surface of the last phalanges of the fingers and toes, the lips, the upper eyelids, the lining of the prepuce, and the glans penis. Some of the hairs are long, others are short and stiff, and others are fine and downy. These differences have led to a division of the hairs into three varieties:

The first variety includes the long, soft hairs, which are found on the head, on the face in the adult male, around the genital organs and under the arms in both the male and the female, and sometimes upon the breast and over the general surface of the body and extremities, particularly in the male.

The second variety, the short, stiff hairs, is found at the entrance of the nostrils, upon the edges of the eyelids, and upon the eyebrows.

The third variety, the short, soft, downy hairs, are found on the general surface not occupied by the long hairs, and in the caruncula lachrymalis. In early life, and ordinarily in the female at all ages, the trunk and extremities are covered with downy hairs; but, in the adult male, these frequently become developed into long, soft hairs.

The hairs are usually set obliquely in the skin and take a definite direction as they lie upon the surface. Upon the head and face, and, indeed, the entire surface of the body, the general course of the hairs may be followed out, and they present currents or sweeps that have nearly always the same direction.

The diameter and length of the hairs are exceedingly variable in different persons, especially in the long, soft hairs of the head and beard. It may be stated in general terms that the long hairs attain the length of from twenty inches to three feet, in women, and considerably less in men. There are instances, however, in women, in which the hairs of the head measure considerably more than three feet, but these are quite unusual. Like the nails, the hair, when left to itself, attains in three or four years a definite length, but when it is habitually cut it grows constantly. The short, stiff hairs are from one quarter to one half an inch in length. The soft, downy hairs measure ordinarily from one-twelfth to one-half an inch. Hairs that have never been cut terminate in pointed extremities; and sometimes in hairs that have been cut, the ends become somewhat pointed, although they are never so sharp as in the new hairs.

Of the long hairs, the finest are upon the head, where they average about $\frac{1}{400}$ of an inch in diameter, the extremes being from $\frac{1}{1500}$ to $\frac{1}{500}$ of an inch for the finest, and from $\frac{1}{400}$ to $\frac{1}{140}$ of an inch for the coarsest. The hair is ordinarily coarser in women than in men. Dark hair is generally coarser than light hair; and, upon the same head, the extremes of variation are sometimes observed. The hairs of the beard and the long hairs of the body are coarser than the hairs of the head. Wilson estimates that the average number of hairs upon a square inch of the scalp is about 1,000, and the number upon the entire head, about 120,000.

The short, stiff hairs are from $\frac{1}{400}$ to $\frac{1}{170}$ of an inch in diameter, and the fine, downy hairs, from $\frac{1}{2000}$ to $\frac{1}{1200}$ of an inch. The variations in the color of the hairs in different races and in different individuals of the same race are sufficiently familiar.

When the hairs are in a perfectly normal condition, they are very elastic and may be stretched to from one-fifth to one-third more than their original length. Their strength varies with their thickness, but an ordinary hair from the head will bear a weight of six or seven ounces. A well-known property of the hair is that of becoming strongly electric by friction; and this is particularly well-marked when the weather is cold and dry. The electricity thus excited is negative. Sections of the shaft of the hairs show that they are oval, but their shape is very variable, straight hairs being nearly round, while curled hairs are quite flat. Another peculiarity of the hairs is that they are strongly hygrometric. They readily absorb moisture and become sensibly elongated, a property which has been made use of by physicists in the construction of delicate hygrometers.

Roots of the Hairs and Hair-follicles.—The roots of the hairs are embedded in follicular openings in the skin, which differ in the different varieties only in the depth to which they penetrate the cutaneous structure. In the downy hairs, the roots pass only into the superficial layers of the true skin; but, in the thicker hairs, the roots pass through the skin and penetrate the subcutaneous cellulo-adipose tissue.

The root of the hair is softer, rounder, and a little larger than the shaft. It becomes enlarged into a rounded bulb at the bottom of the follicle and rests upon a fungiform papilla, constricted at its base, to which it is closely attached. In describing the connection between the hairs and the skin, anatomists mention three membranes forming the walls of the hair-follicles, and two membranes that envelop the roots of the hair in the form of a sheath. The study of these parts is much simplified by keeping constantly in view the correspondence between the different layers of the follicles and the layers of the true skin, and the relations of the root-sheaths with the epidermis.

The follicles are tubular inversions of the structures that compose the corium, and their walls present three membranes. Their length is from $\frac{1}{12}$ to $\frac{1}{4}$ of an inch. The

FIG. 107.—*Hair and hair-follicle.* (Sappey.)
1, root of the hair; 2, bulb of the hair, covering the papilla of the hair-follicle; 3, internal root-sheath; 4, external root-sheath; 5, membrane of the hair-follicle, composed of fusiform, nucleated fibres arranged transversely (the internal, amorphous membrane of the follicle is very delicate and is not represented in the figure); 6, external membrane of the follicle, composed chiefly of longitudinal fibres; 7, 7, muscular bands attached to the follicle; 8, 8, extremities of these bands passing to the skin; 9, compound sebaceous gland, with its duct (10) opening into the upper third of the follicle; 11, simple sebaceous gland; 12, opening of the hair-follicle.

FIG. 108.—*Root of the hair.* (Sappey.)
1, root of the hair; 2, hair-bulb; 3, papilla of the follicle; 4, opening of the follicle; 5, 5, internal root-sheath; 6, external root-sheath; 7, 7, sebaceous glands; 8, 8, excretory ducts of the sebaceous glands.

membrane that forms the external coat of the follicles is composed of inelastic fibres, arranged for the most part longitudinally, provided with blood-vessels and a few nerves, containing some fibro-plastic elements, but deprived entirely of elastic tissue. This is the thickest of the three membranes and is closely connected with the corium. Next to this, is a fibrous membrane composed of fusiform, nucleated fibres arranged transversely. These resemble the non-striated muscular fibres. The internal membrane is structureless and corresponds to the amorphous layer of the true skin. The papilla at the bottom of the hair-sac varies in size with the size of the hairs and is connected with the fibrous layers of the walls of the follicle. It is composed of amorphous matter, with a few granules and nuclei, and it probably contains blood-vessels and nerves, although these are not very distinct.

Although the different membranes of the hair-follicles are sufficiently recognizable, it is evident that the hair-sac is nothing more than an inversion of the corium, with some slight modifications in the character and arrangement of its anatomical elements. The fibrous membranes correspond to the deeper layers of the true skin, without the elastic elements, and they present a peculiar arrangement of its inelastic fibres, the external fibres being longitudinal and the internal fibres transverse. The structureless membrane corresponds to the upper layers of the true skin, which are composed chiefly of amorphous matter. The hair-papilla corresponds to the papillæ on the general surface of the corium.

The investment of the root of the hair presents two distinct layers called the external and internal root-sheaths. The external root-sheath is three or four times as thick as the inner membrane, and it corresponds exactly with the Malpighian layer of the epidermis. This sheath is continuous with the bulb of the hair. The internal root-sheath is a transparent membrane, composed of flattened cells, mostly without nuclei. This extends from the bottom of the hair-follicle and covers the lower two-thirds of the root.

Structure of the Hairs.—The different varieties of hairs present certain peculiarities in their anatomy, but all of them are composed of a fibrous structure forming the greater part of their substance, covered by a thin layer of imbricated cells. In the short, stiff hairs, and in the long, white hairs, there is a distinct medullary substance; but this is wanting in the downy hairs and is indistinct in many of the long, dark hairs.

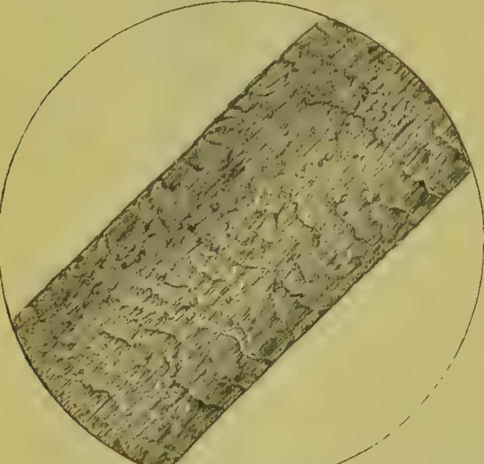


FIG. 109.—*Human hair from the head of a white child; magnified* 370 *diameters.* (From a photograph taken at the United States Army Medical Museum.) This figure shows the imbricated arrangement of the epidermis of the hair.

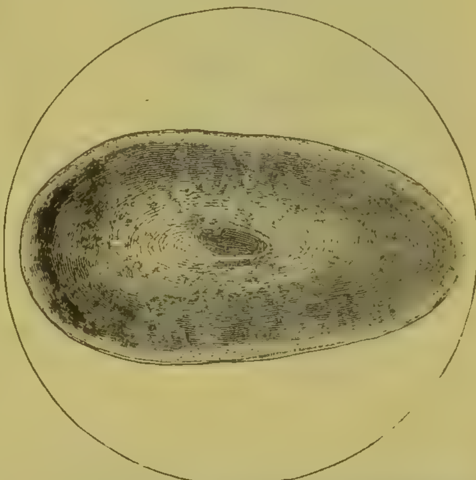


FIG. 110.—*Transverse section of a human hair from the beard of a white adult; magnified* 370 *diameters.* (From a photograph taken at the United States Army Medical Museum.)

The fibrous substance is composed of hard, elongated, longitudinal fibres, which cannot be isolated without the aid of reagents. They may be separated, however, by maceration in warm sulphuric acid, when they present themselves in the form of dark, irregular, spindle-shaped plates, from $\frac{1}{500}$ to $\frac{1}{350}$ of an inch long, and from $\frac{1}{5000}$ to $\frac{1}{3000}$ of an inch wide. These contain pigmentary matter of various shades, occasional cavities filled with air, and a few nuclei. The pigment may be of any color, from a light yellow to an intense black, and it is this substance that gives to the hair the great variety in color which is observed in different persons. In the lower part of the root the fibres are much shorter, and at the bulb they become transformed, as it were, into the soft, rounded cells found in this situation covering the papilla.

The epidermis of the hair is excessively thin and is composed of flattened, quadrangular plates, overlying each other from below upward. These scales, or plates, are without nuclei, and they exist in a single layer over the shaft of the hair and the upper part of its root; but, in the lower part of the root, the cells are thicker, softer, are frequently nucleated, and they exist in two layers.

The medulla is found in the short, stiff hairs, and it is often beautifully distinct in the long, white hairs of the head. It occupies from one-fourth to one-third of the diameter of the hair. The medulla can be traced, under favorable circumstances, from just above the bulb to near the pointed extremity of the hair. It is composed of small, rounded cells, from $\frac{1}{2000}$ to $\frac{1}{1200}$ of an inch in diameter, nucleated, and frequently containing dark granules of pigmentary matter. Mixed with these cells are numerous air-globules; and frequently the cells are interrupted for a short distance and the space is occupied with air. The dark granules of the medullary cells are supposed by Kölliker to be globules of air. The medulla likewise contains a glutinous fluid between the cells and surrounding the air-globules.

Growth of the Hairs.—Although not provided with blood and deprived of sensibility, the hairs are connected with vascular parts and are nourished by imbibition from the papillæ. Each hair is first developed in a closed sac, and at about the sixth month its pointed extremity perforates the epidermis. These first-formed hairs are afterward shed, like the milk-teeth, being pushed out, as it were, by new hairs from below, which arise from a second and a more deeply-seated papilla. This shedding of the hairs usually takes place from two to six months after birth.

The difference in the color of the hair depends upon differences in the quantity and the tint of the pigmentary matter; and, in old age, the hair becomes white or gray from a blanching of the cortex and medulla.

Sudden Blanching of the Hair.—It is an interesting question, in connection with the nutrition of the hair, to examine the instances so often quoted of sudden blanching of the hair from violent emotions or other causes. Some physiologists are of the opinion that the hair may become almost white in the course of a few hours, and this, indeed, is a popular impression; but others assume that such sudden changes never take place, although it is certain that the hair frequently turns gray in the course of a few weeks. In examining the literature of this subject, it is difficult to find, in the older works, well-authenticated cases of these sudden changes, and most of those that have been quoted are taken upon the loose authority of persons evidently not in the habit of making scientific observations. Such instances, unsupported by analogous cases of a reliable character, must necessarily be rejected as not fulfilling the rigid requirements demanded in scientific inquiries, in which all possible sources of error should be carefully excluded. It is not necessary, therefore, to quote the instances of sudden blanching of the hair recorded by the ancient writers, or those well-known cases of later date, so often detailed in scientific works, such as that of Marie Antoinette or Sir Thomas More; and it seems proper to exclude, also, cases in which the blanching of the hair has been observed only by friends or relatives; for in most of them the statements with regard to time are conflicting and unsatisfactory.

Regarding the subject, however, from a purely scientific point of view, there are a few instances of late date, in which sudden blanching of the hair has been observed and the causes of this remarkable phenomenon fully investigated by competent observers; and it is almost unnecessary to say that a single well-authenticated case of this kind demonstrates the possibility of its occurrence and is interesting in connection with the reported instances which have not been subjected to proper investigation. One of these cases is reported in *Virchow's Archiv*, for April, 1866, by Dr. Landois, as occurring under the observation of himself and Dr. Lohmer. In this case, the blanching of the hair occurred in a hospital in a single night, while the patient was under the daily observation of the visiting physician. As this is one of the few well-authenticated instances of sudden blanching of the hair, we shall give, in a few words, its essential particulars:

The patient, a compositor, thirty-four years of age, with light hair and blue eyes, was admitted into the hospital, July 9, 1865, suffering apparently from an acute attack of delirium tremens. A marked peculiarity in the disease was excessive terror when any person approached the patient. He slept for twelve hours on the night of the 11th of July, after taking thirty drops of laudanum. Up to this time nothing unusual had been observed with regard to the hair. On the morning of July 12th, it was evident to the medical attendants and all who saw the patient that the hair of the head and beard had become gray. This fact was also remarked by the friends who visited the patient, and he himself called for a mirror and remarked the change with intense astonishment. The patient continued in the hospital until September 7th, when he was discharged, the hair remaining gray. An interesting point connected with this case is the fact that the hairs were submitted to careful microscopical examination. The white hairs were found to contain a great number of air-globules in the medulla and in the cortical substance, but the pigment was everywhere preserved. The presence of air gave the hairs a dark appearance by transmitted light and a white appearance by reflected light. Dr. Landois quotes, in this connection, instances of blanching of the hair, in which each hair presented alternate rings of a white and a brown color. Another very curious case of this kind was lately reported to the Royal Society by Mr. Erasmus Wilson. In this case, the white portions presented, on microscopical examination, great bubbles of air; but there was no diminution in the quantity of pigmentary matter.

The microscopical examinations by Dr. Landois and others leave no doubt as to the cause of the white color of the hair in cases of sudden blanching; and the instances we have just quoted show that the fact of the occurrence of this phenomenon can no longer be called in question. All are agreed that there is no diminution in the pigment, but that the greater part of the medulla becomes filled with air, small globules being also found in the cortical substance. The hair in these cases presents a marked contrast with hair that has become gray gradually from old age, when there is always a loss of pigment in the cortex and medulla. How the air finds its way into the hair in sudden blanching, it is difficult to imagine; and the views that have been expressed on this subject by different authors are entirely theoretical.

The fact that the hair may become white or gray in the course of a few hours renders it probable that many of the cases reported upon unscientific authority actually occurred; and these have all been supposed to be connected with intense grief or terror. The terror was very marked in the case reported by Dr. Landois. In the great majority of recorded observations, the sudden blanching of the hair has been apparently connected with intense mental emotion; but this is all that can be said on the subject of causation, and the mechanism of the change is not understood.

Uses of the Hairs.—The hairs serve an important purpose in the protection of the general surface and in guarding certain of the orifices of the body. The hair upon the head and the face protects from cold and shields the head from the rays of the sun during exposure in hot climates. Although the amount of hair upon the general surface is small, as it is a very imperfect conductor of caloric, it serves in a degree to maintain the heat of the body. It also moderates the friction upon the surface. The eyebrows prevent the perspiration from running from the forehead upon the lids; the eyelashes protect the surface of the conjunctiva from dust and other foreign matters; the mustache protects the lungs from dust, a function very important in persons exposed to dust in long journeys or in their daily work; and the short, stiff hairs at the openings of the ears and nose protect these orifices. It is difficult to assign any special office to the hairs in some other situations, but their general uses are sufficiently evident.

Perspiration.

In the fullest acceptation of the term, perspiration embraces the entire function of the skin as an excreting organ and includes the exhalation of carbonic acid as well as of watery vapor and organic matter. The office of the skin as an eliminator is undoubtedly very important; but the quantity of excrementitious matters with the properties of which we are well acquainted, such as carbonic acid and urea, thrown off from the general surface is small as compared with the amount exhaled by the lungs and discharged by the kidneys. If the surface of the body be covered with an impermeable coating, death occurs in a very short time; but the phenomena which precede the fatal result are difficult to explain. All that we can say upon this point is that death takes place when the heat of the body has been reduced to about 70° Fahr., and that suppression of the function of the skin in this way is always followed by a depression of the animal temperature. The cause of death has never been satisfactorily explained, partly for the reason that we are unacquainted with the nature and properties of all the excrementitious matters exhaled from the skin; and it is not easy to understand why coating the surface should be followed by such a rapid diminution in the general temperature. The experimental facts, however, indicate that the skin probably possesses important functions with which we are entirely unacquainted. Physiological chemists have detected urea and some other effete matters in the perspiration, but it is probable that some volatile principles are eliminated by the general surface, which have thus far escaped observation.

Sudoriparous Glands.—The most numerous and the most important glands of the skin are those which secrete the sweat. The other glands, which have been already considered, have rather a mechanical function, serving to keep the skin and its appendages in a proper condition for the protection of the subjacent parts; but it is the perspiratory apparatus chiefly which is concerned in the great function of elimination.

With few exceptions, every portion of the skin is provided with sudoriparous glands. They are not found, however, in the skin covering the concave surface of the concha of the ear, the glans penis, the inner lamella of the prepuce, and, unless the ceruminous glands be regarded as sudoriparous organs, in the external auditory meatus.

On examining the surface of the skin with a low magnifying power, especially on the palms of the hands and the soles of the feet, the orifices of the sudoriferous ducts may be seen in the middle of the papillary ridges, forming a regular line in the shallow groove between the two rows of papillæ. The tubes always open upon the surface obliquely. If a thin section of the skin be carefully made and examined microscopically, the ducts are seen passing through the different layers and terminating in rounded, convoluted coils in the subcutaneous structure. These little, rounded or ovoid bodies, which constitute the sudoriparous, or sweat-producing apparatus, may be seen attached to the under surface of the skin, when it has been removed from the subjacent parts by maceration. The perspiratory apparatus consists, indeed, of a simple tube, presenting a coiled mass beneath the skin, the sudoriparous portion, and a tube of greater or less length, in proportion to the thickness of the cutaneous layers, which is the excretory duct, or the sudoriferous portion.

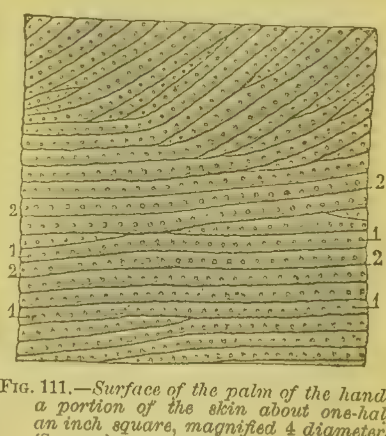


FIG. 111.—*Surface of the palm of the hand; a portion of the skin about one-half an inch square, magnified 4 diameters.* (Sappey.)

1, 1, 1, 1, openings of the sudoriferous ducts; 2, 2, 2, 2, grooves between the papillæ of the skin.

The glandular coils vary in size from $\frac{1}{125}$ to $\frac{1}{25}$ of an inch; the smallest coils being found beneath the skin of the penis, the scrotum, the eyelids, the nose, and the convex surface of the concha of the ear, and the largest, on the areola of the nipple and the perineum. Very large glands are found mixed with smaller ones in the axilla, but these produce a peculiar secretion which will be specially considered. The coiled portion of the tube is about $\frac{1}{370}$ of an inch in diameter and forms from six to twelve convolutions. It consists of a sharply-defined, strong, external membrane, from $\frac{1}{6000}$ to $\frac{1}{3500}$ of an inch in thickness, very transparent, uniformly granular, and sometimes indistinctly striated. This is of uniform diameter throughout the coil and terminates in a very slightly dilated, rounded, blind extremity. It is filled with epithelium in the form of finely granular matter, usually not segmented into cells, and provided with small, oval nuclei. The glandular mass is surrounded by a plexus of capillary blood-vessels, which send a few small branches between the convolutions of the coil. Sometimes the coil is enclosed in a delicate fibrous envelope.

The excretory duct is simply a continuation of the glandular coil. Its course through the layers of the true skin is nearly straight. It then passes into the epidermis between the papillæ of the corium, and presents, in this layer, a number of spiral turns. The spirals vary in number according to the thickness of the epidermis. Sappey has found from six to ten in the palms of the hands and from twelve to fifteen in the soles of the feet. As it emerges from the glandular coil, the excretory duct is somewhat narrower than the tube in the secreting portion; but, as it passes through the epidermis, it again becomes larger. It possesses the same external membrane as the glandular coil and is lined generally by two layers of cells of pavement-epithelium.

FIG. 112.—*Sudoriparous glands; magnified 20 diameters.* (Sappey.)
1, 1, epidermis; 2, 2, mucous layer; 3, 3, papillæ; 4, 4, derma; 5, 5, subcutaneous areolar tissue; 6, 6, 6, 6, sudoriparous glands; 7, 7, adipose vesicles; 8, 8, excretory ducts in the derma; 9, 9, excretory ducts divided.

In a section of the skin and the subcutaneous tissue, involving several of the sudoriparous glands with their ducts, it is seen that the glandular coils are generally situated at different planes beneath the skin, as is indicated in Fig. 112.

Robin has described a variety of sudoriparous glands in the axilla, which do not differ so much from the glands in other parts in their anatomy as in the character of their secretion. The coil in these glands is much larger than in other parts, measuring from $\frac{1}{25}$ to $\frac{1}{12}$ of an inch; the walls of the tube are thicker, and they present an investment of fibrous tissue with an internal layer of longitudinal, unstriped muscular fibres; and, finally, the tubes of the coil itself are lined with cells of pavement-epithelium. They are very numerous in the axilla, forming a continuous layer beneath the skin. Mixed with these, are a few glands of the ordinary variety.

Estimates have been made by different writers of the absolute number of sudoriparous glands in the body and the probable extent of the exhalant surface of the skin. One of the most careful, and probably the most reliable of these estimates, is that made by Krause; but, like all estimates of this kind, the results are to be taken as merely approximative. Krause found great differences in the number of perspiratory openings in different portions of the skin, and he estimated the number in a square inch in certain parts, as follows: On the forehead, he found 1,258 glands to a square inch; on the cheeks, 548; on the anterior and lateral portions of the neck, 1,303; on the breast and abdomen, 1,136; on the back of the neck, the back, and the nates, 417; on the fore-arm, inner surface, 1,123, and the outer surface, 1,093; on the hand, palmar surface, 2,736, and dorsal surface, 1,490; on the upper part of the thigh, inner surface, 576, outer surface, 554; on the lower part of the thigh, inner surface, 576; on the foot, plantar surface, 2,685, and dorsal surface, 924. From these figures, it is estimated that the entire number of perspiratory glands is 2,381,248; and, assuming that each coil when unravelled measures about $\frac{1}{16}$ of an inch, the entire length of the secreting tubes is about $2\frac{1}{4}$ miles. It must be remembered, however, that the length of the secreting coil only is given, and that the excretory ducts are not included.

Mechanism of the Secretion of Sweat.—The action of the skin as a glandular organ is continuous and not intermittent; but, under ordinary conditions, the sweat is exhaled from the general surface in the form of vapor. With regard to the mechanism of its separation from the blood, nothing is to be said in addition to the general remarks upon the subject of secretion; and it is probable that the epithelium of the secreting coils is the active agent in the selection of the peculiar matters which enter into its composition. There are no examples of the separation by glandular organs of vapor from the blood, and the perspiration is secreted as a liquid, and only becomes vaporous as it is discharged upon the surface.

The influence of the nervous system upon the secretion of sweat is remarkable. It is well known, for example, that an abundant production of perspiration is frequently the result of mental emotions. Bernard has shown, in a series of interesting experiments, that the nervous influence may be propagated through the sympathetic system. In one of these observations, he divided the sympathetic in the neck of a horse, producing, as a consequence, an elevation in temperature and an increase in the arterial pressure in the part supplied with branches of the nerve. He found, also, that the skin of the part became covered with a copious perspiration. Upon galvanizing the divided extremity of the nerve, the secretion of sweat was arrested. When the skin is in a normal condition, after exercise or whenever there is a tendency to elevation of the animal temperature, there is a determination of blood to the surface, accompanied with an increase in the secretion of sweat. This is the case when the body is exposed to a high temperature; and it is by an increase in the transpiration from the surface that the animal heat is maintained at the normal standard.

Quantity of Cutaneous Exhalation.—The amount of cutaneous exhalation is subject to great variations, depending upon conditions of temperature and moisture, exercise, the quantity and character of the ingesta, etc. Most of these variations relate to the function of the skin in regulating the temperature of the body; and it is probable that the elimination of excrementitious matters by the skin is not subject, under normal conditions, to the same modifications, although positive experiments upon this point are wanting. It is not designed, in this connection, to discuss all the experiments that have been made upon the quantity and the modifications of the cutaneous exhalations, and we shall consider only what appear to be the most reliable of the numerous recorded observations upon this subject. The classical experiments of Sanctorius were among the first attempts to determine by the balance the relations of the ingesta to the exhalations; but these were necessarily imperfect, on account of the difficulty in constructing proper instruments for the investigations, and the cutaneous and pulmonary exhalations were estimated together. When there is such a wide range of variation in different individuals and in the same person under different conditions of season, climate, etc., it is only possible to give approximate estimates of the quantity of sweat secreted and exhaled in the twenty-four hours; and more recent observations have shown that the calculations of Seguin and Lavoisier, made in 1790, are very nearly correct. These observers estimated the daily quantity of cutaneous transpiration at about two pounds (one pound and fourteen ounces). The estimates of Krause and of Valentin are a little less, but the difference is not considerable.

Under violent and prolonged exercise, the loss of weight by exhalation from the skin and lungs may become very considerable. It is stated by Mr. Maclaren, the author of an excellent work on training, that, in one hour's energetic fencing, the loss by perspiration and respiration, taking the average of six consecutive days, was about three pounds, or, accurately, forty ounces, with a range of variation of eight ounces.

When the body is exposed to a very high temperature, the amount of exhalation from the surface is immensely increased; and it is by this rapid evaporation that persons have been able to endure for several minutes a dry heat considerably exceeding that of boiling water. Dr. Southwood Smith made some very interesting observations with regard to this point upon workmen employed about the furnaces of gas-works and exposed to intense heat; and he found that, in an hour, the loss of weight amounted to from two to four pounds, this being chiefly by exhalation of watery vapor from the skin. In such instances, the loss of water by transpiration is supplied constantly by the ingestion of large quantities of liquid.

Properties and Composition of the Sweat.—A very complete and satisfactory analysis of the sweat was made by Favre, in 1853. After taking every precaution to obtain the secretion in a perfectly pure state, he collected a very large quantity, nearly thirty pints (fourteen litres), the result of six transpirations from one person, which he assumed to represent about the average in composition. The liquid was perfectly limpid, colorless, and of a feeble but characteristic odor. Almost all observers have found the reaction of the sweat to be acid; but it readily becomes alkaline on being subjected to evaporation, showing that it contains some of the volatile acids. In the experiments of Favre, it was found that the fluid collected during the first half-hour of the observation was acid, during the second half-hour it was neutral or feebly alkaline, and during the third half-hour, constantly alkaline. The specific gravity of the sweat is from 1003 to 1004. The following is the composition of the fluid collected by Favre:

Composition of the Sweat.

Water		995·573
Urea		0·043
Fatty matters		0·014
Alkaline lactates		0·317
Alkaline sudorates		1·562
Chloride of sodium,	soluble in water	2·230
Chloride of potassium,	soluble in water	0·244
Alkaline sulphates,	soluble in water	0·012
Alkaline phosphates,	soluble in water	a trace.
Alkaline albuminates,	soluble in water	0·005
Alkaline earthy phosphates (soluble in acidulated water)		a trace.
Epidermic *débris* (insoluble)		a trace.
		1,000·000

We have already alluded to the functions of the skin as a respiratory organ and its office in regulating the temperature of the body by the evaporation of what is known as the insensible perspiration; but the composition of the sweat indicates clearly that the skin is an important organ of excretion. Urea is now known to be a constant constituent of the sweat, and the compounds of sudoric acid are probably excrementitious in their character, although they have not yet been detected in the blood or in any of the tissues. The quantity of urea, under ordinary conditions, is not large; but it is well known that its proportion in the sweat is very much increased when there is deficient elimination by the kidneys. The sudoric acid, obtained by decomposition of the sudorates of soda and of potassa, is a nitrogenized substance, with a formula, according to Favre, who first described it, of $C_{10}H_8O_{13}N$. The nature of the volatile acid has not yet been determined. The fatty matters are probably produced by the sebaceous glands, and the ordinary nitrogenized matters are derived from the epidermic scales. With regard to the inorganic constituents, there is no great interest attached to any but the chloride of sodium, which exists in a proportion many times greater than that of all the other inorganic matters combined.

Peculiarities of the Sweat in Certain Parts.—In the axilla, the inguino-scrotal region in the male, and the inguino-vulvar region in the female, and between the toes, the sweat always has a peculiar odor, more or less marked, which, in some persons, is excessively disagreeable. Donné has shown that whenever the secretion has an odor of this kind its reaction is distinctly alkaline; and he is disposed to regard its peculiar characters as due to a mixture of the secretion of the other follicles found in these situations. Sometimes the sweat about the nose has an alkaline reaction. In the axillary region, the secretion is rather less fluid than on the general surface and frequently has a yellowish color, so marked, sometimes, as to stain the clothing. The odor is probably due to the presence of volatile, odorous compounds of the fatty acids, like the caproates, the valerates, or the butyrates; but the presence of these principles has never been accurately determined.

Physiological Anatomy of the Kidneys.

The urine is generally regarded by physiologists as the type of the excrementitious fluids, it having no function to perform in the economy, but being simply retained in the bladder to be voided at convenient intervals. All the remarks, indeed, that have been made concerning excretion in general may be applied without reserve to the action of the kidneys; and there are few subjects in physiology of greater interest than the process of urinary excretion, with its relations to nutrition and disassimilation. In entering upon the study of the functions of the kidneys, it will be found useful to consider certain points in their anatomy.

The kidneys are symmetrical organs, situated in the lumbar region beneath the peritoneum, invested by a proper fibrous coat, and always surrounded by more or less adipose tissue. They usually extend from the eleventh or twelfth rib downward to near the crest of the ilium, and the right is always a little lower than the left. In shape, the kidney is very aptly compared to a bean; and the concavity, the deep, central portion which is called the hilum, looks inward toward the spinal column. The weight of each kidney is from four to six ounces, usually about half an ounce less in the female than in the male. The left kidney is nearly always a little heavier than the right.

Outside of the proper coat of the kidney, is a certain amount of fatty tissue enclosed in a loose fibrous structure. This is sometimes called the adipose capsule; but the proper coat consists of a close net-work of the ordinary white fibrous tissue, interlaced with numerous small fibres of the elastic variety. This coat is thin and smooth and may be readily removed from the surface of the organ. At the hilum, it is continued inward to line the pelvis of the kidney, covering the calices and blood-vessels. This coat, however, is not continued into the substance of the kidney.

On making a vertical section of the kidney, it presents a cavity at the hilum, bounded externally by the dilated origin of the ureter. This is called the pelvis. It is lined by a smooth membrane, which is simply a continuation of the proper coat of the kidney, and which forms little cylinders, called calices, into which the apices of the pyramids are received. Some of the calices receive the apex of a single pyramid, while others are larger and receive two or three. The calices unite into three short, funnel-shaped tubes, called infundibula, corresponding respectively to the superior, middle, and inferior portions of the kidney. These finally open into the common cavity, or pelvis. The substance of the kidney is composed of two distinctly-marked portions called the cortical substance, and the medullary, or pyramidal substance.

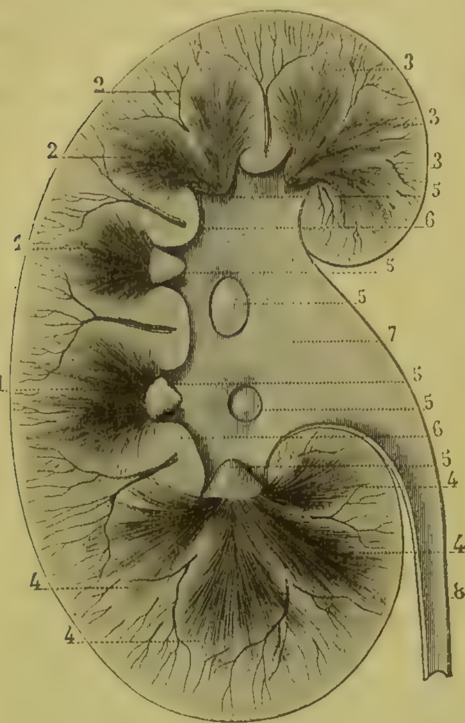


FIG. 113.—*Vertical section of the kidney.* (Sappey.) 1, 1, 2, 2, 3, 3, 4, 4, 4, 4, pyramids of Malpighi; 5, 5, 5, 5, 5, 5, apices of the pyramids surrounded by the calices; 6, 6, columns of Bertin; 7, pelvis of the kidney; 8, upper extremity of the ureter.

The cortical substance is reddish and granular, rather softer than the pyramidal substance, and is about one-sixth of an inch in thickness. This occupies the exterior of the kidney and sends little prolongations (columns of Bertin) between the pyramids. The surface of the kidney is marked by little polygonal divisions, giving it a lobulated appearance. This, however, is simply due to the arrangement of the superficial blood-vessels. The medullary substance is arranged in the form of pyramids, sometimes called the pyramids of Malpighi, from twelve to fifteen or eighteen in number, their bases presenting toward the cortical substance, and their apices being received into the calices at the pelvis. Ferrein subdivided the pyramids of Malpighi into smaller pyramids (the pyramids of Ferrein), each formed by about one hundred tubes radiating from the openings at the summit of the pyramids toward their bases. The tubes composing these pyramids were supposed to pass into the cortical substance, forming corresponding pyramids of convoluted tubes, thus dividing this portion of the kidney into lobules, more or less distinct. The medullary substance is firm, of a darker red color than the cortical substance, and is marked by tolerably distinct striæ, which take a nearly straight course from the bases to the apices of the pyramids. As these striæ indicate the direction of the little tubes that constitute the greatest part of the medullary substance, this is sometimes called the tubular portion of the kidney.

From the arrangement of the secreting portion of the kidneys, they are classed among the tubular glands, presenting a system of tubes, or canals, some of which are supposed simply to carry off the urine, while others separate the excrementitious constituents of this fluid from the blood. It is difficult to determine precisely where the secreting tubes merge into the excretory ducts, but it is the common idea, which is probably correct, that the cortical substance is the active portion, while the tubes of the pyramidal portion simply carry off the excretion.

Pyramidal Substance.—Each papilla, as it projects into the pelvis of the kidney, presents from ten to twenty-five little openings, measuring from $\frac{1}{300}$ to $\frac{1}{60}$ of an inch in diameter. The tubes leading from the pelvis immediately divide at very acute angles, generally dichotomatously, until a bundle of tubes arises, as it were, from each opening. These bundles constitute the pyramids of Ferrein. In their course, the tubes are slightly wavy and are nearly parallel with each other. These are called the straight tubes of the kidney, or the tubes of Bellini. They extend from the apices of the pyramids to their bases and pass then into the cortical substance. The pyramids contain, in addition to the straight tubes, a delicate fibrous matrix and numerous blood-vessels; which latter, for the most part, pass beyond the pyramids, to be finally distributed in the cortical substance. Recent researches have shown that some of the convoluted tubes dip down into the pyramids, returning to the cortical substance in the form of loops. This arrangement will be fully described in connection with the cortical substance.

The tubes of the pyramidal substance are composed of a strong, structureless basement-membrane, lined with granular, nucleated cells. According to the researches of Bowman, the tubes measure from $\frac{1}{300}$ to $\frac{1}{200}$ of an inch in diameter at the apices, and near the bases of the pyramids their diameter is about $\frac{1}{600}$ of an inch. The membrane of the tubes is dense and resisting, and portions of it with the epithelial lining removed can generally be seen in microscopical examinations, when the pyramidal substance has been simply lacerated with needles. This membrane is from $\frac{1}{30000}$ to $\frac{1}{20000}$ of an inch in thickness.

The cells lining the straight tubes exist in a single layer applied to the basement-membrane. They are thick, irregularly polygonal in shape, and contain numerous albuminoid granules. They present one, and occasionally, though rarely, two granular nuclei, with one or two nucleoli. They are very liable to alteration and are only seen in the

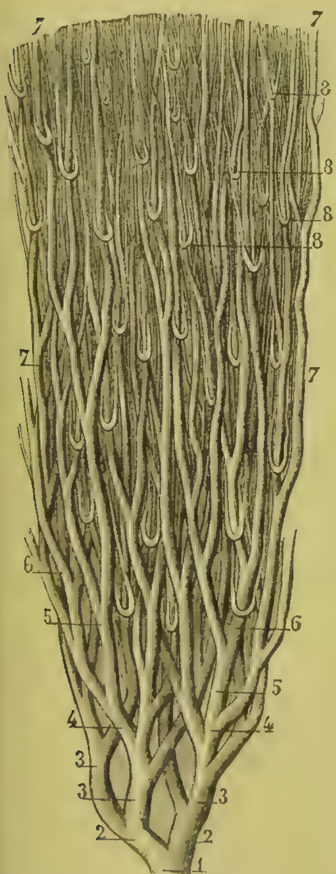


FIG. 114 (A).—*Longitudinal section of the pyramidal substance of the kidney of the fœtus.* (Sappey.)

1, trunk of a large uriniferous tube; 2, 2, primary branches of this tube; 3, 3, 3, secondary branches; 4, 4, 5, 5, 6, 6, 7, 7, 7, 7, branches becoming smaller and smaller; 8, 8, 8, 8, loops of the tubes of Henle.

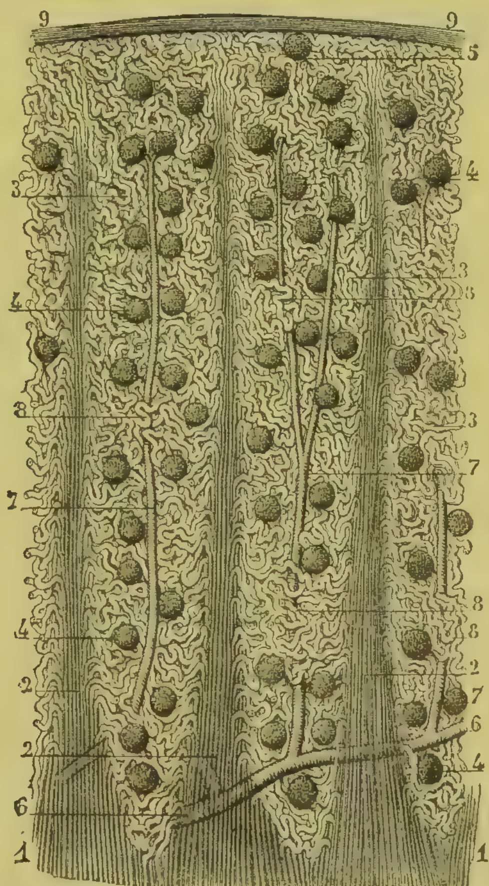


FIG. 114 (B).—*Longitudinal section of the cortical substance of the same kidney.* (Sappey.)

1, 1, limit of the cortical substance and base of the pyramids; 2, 2, 2, tubes passing toward the surface of the kidney; 3, 3, 3, 8, 8, 8, convoluted tubes; 4, 4, 4, 4, 5, Malpighian bodies; 6, 6, artery, with its branches (7, 7, 7); 9, 9, fibrous covering of the kidney.

normal condition in a perfectly fresh, healthy kidney. Their diameter is about $\frac{1}{1500}$ of an inch. The caliber of the tubes is reduced by the thickness of their lining epithelium to $\frac{1}{900}$ or $\frac{1}{800}$ of an inch.

Cortical Substance.—In the cortical portion of the kidney, are found numerous tubes, differing somewhat from the tubes of the pyramidal portion in their size and in the character of their epithelial lining, but presenting the most marked difference in their direction. These tubes are somewhat larger than the tubes of pyramidal substance and are very much convoluted, interlacing with each other inextricably in every direction. Scattered pretty uniformly throughout this portion of the kidney, are rounded or ovoid bodies, about four times the diameter of the convoluted tubes, known as the Malpighian bodies. At one time there was considerable difference of opinion with regard to the relation of these bodies to the tubes; but the researches of Bowman, Isaacs, and later anatomists, have established, without doubt, the fact that they are simply flask-like, terminal dilatations of the tubes themselves.

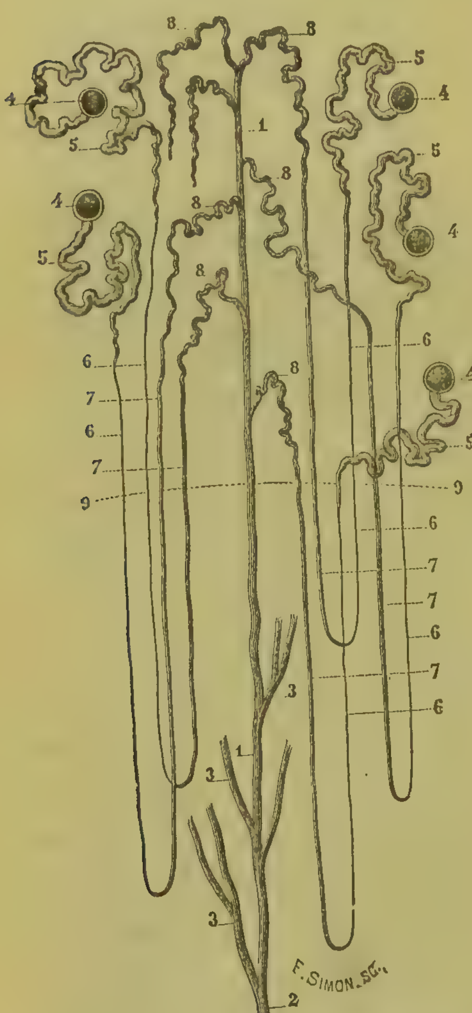


FIG. 115.—*Diagrammatic view of the Malpighian bodies and tubes of the kidney.* (Sappey.)
1, 1, 2, straight tube of Bellini; 3, 3, 3, other straight tubes opening into the tube 1, 1; 4, 4, 4, 4, 4, Malpighian bodies; 5, 5, 5, 5, 5, convoluted tubes; 6, 6, 6, 6, 6, descending portions of the looped tubes of Henle; 7, 7, 7, 7, 7, ascending, larger portions of the tubes of Henle; 8, 8, 8, 8, 8, 8, communicating tubes; 9, 9, dotted line showing the limits of the cortical and of the pyramidal substance.

As the result of recent researches, the cortical portion of the kidney is now regarded as presenting a delicate fibrous matrix, which forms a sort of skeleton for the support of the secreting portion with its blood-vessels. The tubes of this portion are convoluted and somewhat larger than the straight tubes, but are continuous with them, terminating finally in the Malpighian bodies. The researches of late anatomists, however, particularly in Germany, have shown that this simple view of the course and termination of the tubes of the cortical substance must be somewhat modified; although, as far as the anatomy of the organ has any bearing upon our ideas concerning the mechanism of the secretion of urine, the views of physiologists need undergo no material change.

The tubes of the cortical substance present considerable variations in size, and, instead of a single system continuous with the straight tubes and terminating in the Malpighian bodies, we can distinguish three well-defined varieties:

1. The ordinary convoluted tubes, directly connected with the Malpighian bodies. 2. Small tubes, continuous with the convoluted tubes, dipping down into the pyramids and returning to the cortical portion in the form of loops. 3. Large, communicating tubes, forming a plexus connecting the different varieties of tubes with each other and finally with the straight tubes of the pyramidal portion.

The relation of these tubes can be readily understood by reference to Fig. 115. In tracing out the course of the tubes, which recent observations have shown to be somewhat intricate, it will be found most convenient to commence with a description of the Malpighian bodies and to follow the course of the tubes from these bodies to their connections with the straight tubes of the pyramidal substance.

Malpighian Bodies.—These are ovoid or rounded terminal dilatations of the convoluted tubes, of somewhat variable size, measuring from $\frac{1}{250}$ to $\frac{1}{100}$ of an inch in diameter. They are composed of a membrane continuous with the external membrane of the convoluted tubes, of the same homogeneous character, but somewhat thicker, measuring about $\frac{1}{25000}$ of an inch, while the membrane of the tubes is only about $\frac{1}{10000}$ of an inch in thickness. This sac, which is sometimes called the capsule of Müller, encloses a mass of convoluted blood-vessels and is lined with a layer of nucleated epithelial cells. In addition to these pale, delicate cells lining the capsule, there are other cells which are applied to the blood-vessels. These latter cells are probably concerned in the elimination of the solid constituents of the urine.

The cells attached to the capsule of Müller are smaller and more transparent than those lining the convoluted tubes. They are ovoid, nucleated, and finely granular. The cells covering the vessels, however, are larger and more opaque, and they resemble the epithelium lining the tubes. They measure from $\frac{1}{1400}$ to $\frac{1}{1000}$ of an inch in diameter, by about $\frac{1}{2500}$ of an inch in thickness.

Tubes of the Cortical Substance.—Following out the tubes in the cortical substance from the Malpighian bodies, we find first a short, constricted portion, which is sometimes called the neck of the capsule. The tube soon dilates to the diameter of about $\frac{1}{500}$ of an inch, when its course becomes exceedingly intricate and convoluted. These are what are known as the convoluted tubes of the kidney. The membrane of these tubes is transparent and homogeneous, but quite firm and resisting. It measures about $\frac{1}{40000}$ of an inch in thickness. It is lined throughout with a single layer of rounded or irregularly polygonal epithelial cells, from $\frac{1}{1400}$ to $\frac{1}{1000}$ of an inch in diameter, somewhat larger, consequently, than the cells lining the straight tubes. These cells are nucleated and usually quite granular. It has been found that, in many of the lower orders of animals, the cells lining the neck of the capsule are provided with vibratile cilia; and it is possible that they may exist in man, although their presence has never been actually demonstrated.

The course of the tubes, after they have lost the characters which were formerly supposed to be peculiar to the tubes of the cortical substance, and their anastomoses, have attracted much attention within the last few years. It has been shown by Henle, and the most important points in his observations have been confirmed by numerous anatomists, that the convoluted tubes, instead of connecting directly with the tubes of the pyramidal substance, are continuous with a system of smaller tubes, which pass into the pyramids in the form of loops.

Narrow Tubes of Henle.—According to the most recent observations, the convoluted tubes above described, after a long and tortuous ramification in the cortical substance, invariably become continuous, near the pyramids, with tubes of much smaller diameter, which form loops, extending to a greater or less depth into the pyramids. The loops formed by these canals (the narrow tubes of Henle) are nearly parallel with the tubes of Bellini and are much more numerous near the bases of the pyramids than toward the apices. The diameter of these tubes is very variable, and they present enlargements at irregular intervals in their course. The narrow portions are about $\frac{1}{2000}$ of an inch in diameter, and the wide portions, about twice this size. The narrow portion is lined by small, clear cells with very prominent nuclei. The wider portions are lined by larger, granular cells. Near the bases of the pyramids, the wide portion sometimes forms the loop; but, near the apices, the loop is always narrow. The difference in the size of the epithelium is such, that, while the diameter of the tube is variable, its caliber remains nearly uniform. The membrane of these tubes is quite thick, thicker, even, than the membrane of the tubes of Bellini.

Intermediate Tubes.—After the narrow tubes of Henle have returned to the cortical substance, they communicate with a system of flattened, ribbon-shaped canals, measuring from $\frac{1}{1200}$ to $\frac{1}{1000}$ of an inch in diameter, with excessively thin, fragile walls, lined by clear pavement-epithelium. These tubes take an irregular and somewhat angular course between the true convoluted tubes and finally empty into the branches of the straight tubes of Bellini, thus establishing a communication between the tubes coming from the Malpighian bodies and the tubes of the pyramidal substance. They are called the inter-mediate tubes, or the canals of communication. Some observers have described them as forming an anastomosing plexus, but this disposition is not definitely established.

The tubes into which the intermediate canals open join with others, generally two by two, and then pass in a nearly straight direction into the pyramids, where they continue to unite with each other in their course, becoming, consequently, less and less numerous, until they open at the apices of the pyramids into the infundibula and the pelvis of the kidney.

Distribution of Blood-vessels in the Kidney.—The renal artery, which is quite voluminous in proportion to the size of the kidney, enters at the hilum and divides into four branches. By numerous smaller branches it then penetrates between the pyramids and ramifies in the columns of cortical substance which occupy the spaces between the pyramids (columns of Bertin). The main vessels, which are generally two in number, occupy the centre of the columns of Bertin, sending off in their course, at short intervals, regular branches on either side, toward the pyramids. When these branches reach the boundary of the cortical substance, they turn upward and follow the periphery of the pyramid to its base. Here the vessels form an arched, anastomosing plexus, situated exactly at the boundary which separates the rounded base of the pyramid from the cortical substance. This plexus presents a convexity looking toward the cortical substance, and a concavity, toward the pyramid. It is so arranged that the interstices are just large enough to admit the collections of tubes that form the so-called pyramids of Ferrein.

From the arterial arcade, branches are given off in two opposite directions. From its concavity, numerous small branches, measuring at first from $\frac{1}{1200}$ to $\frac{1}{150}$ of an inch in diameter, pass downward toward the papillæ, giving off small ramifications at very acute angles and becoming reduced in size to about $\frac{1}{2500}$ of an inch. These vessels—called sometimes the arteriolæ rectæ—surround the straight tubes and pass into capillaries in the substance of the pyramids and at their apices.

From the convex surface of the arterial arcade, numerous branches are given off at nearly right angles. These pass into the cortical substance, breaking up into a large number of little arterial twigs, from $\frac{1}{1500}$ to $\frac{1}{600}$ of an inch in diameter, each one of which penetrates a Malpighian body at a point opposite to the origin of the convoluted tube. Once within the capsule, the arteriole breaks up into from five to eight branches, which then divide dichotomatously into vessels measuring from $\frac{1}{3000}$ to $\frac{1}{1500}$ of an inch in diameter, arranged in the form of coils and loops, constituting a dense, rounded mass (the Malpighian coil), filling the capsule. These vessels break up into capillaries without anastomoses. Their coats are amorphous and are provided with numerous nuclei rather shorter than those found in the general capillary system.

The blood is collected from the vessels of the Malpighian bodies by veins, sometimes one, and frequently three or four, which pass out of the capsule and form a second capillary plexus surrounding the convoluted tubes. When there is but one vein, it generally emerges from the capsule near the point of penetration of the arteriole. The walls of the vein are much more fragile than those of the arteriole, and, consequently, in ordinary microscopical preparations of the cortical substance, the arteriole is left attached, while the veins are torn off.

The efferent vessels, immediately after their emergence from the capsule, break up into a very fine and delicate plexus of capillaries, closely surrounding the convoluted tubes. These form a true plexus, the branches anastomosing freely in every direction; and the distribution of vessels in this part resembles essentially the vascular arrangement in most of the glands. Bowman has called the branches which connect together the vessels of the Malpighian tuft and the capillary plexus surrounding the tubes, the portal system of the kidney. These intermediate vessels form a coarse plexus surrounding the prolongations of the pyramids of Ferrein into the cortical substance.

The renal, or emulgent vein takes its origin in part from the capillary plexus surrounding the convoluted tubes and in part from the vessels distributed in the pyramidal substance. A few branches come from vessels in the envelopes of the kidney, but these are comparatively unimportant. The plexus surrounding the convoluted tubes empties into venous radicles, which pass to the surface of the kidney, and these present a number of little radiating groups, each converging toward a central vessel. This arrangement gives to the vessels of the fibrous envelope of the kidney a peculiar stellate appearance. These are sometimes called the stars of Verheyn. The large trunks which form the centres of these stars then pass through the cortical substance to the rounded bases of the pyramids, where they form a vaulted, venous plexus corresponding to the arterial plexus already described. The vessels distributed upon the straight tubes of the pyramidal substance form a loose plexus around these tubes, except at the papillæ, where the network is much closer. They then pass into the plexus at the bases of the pyramids to join with the veins from the cortical substance. From this plexus, a number of larger trunks arise and pass toward the hilum in the centre of the inter-pyramidal substance, enveloped in the same sheath with the arteries. Passing thus to the pelvis of the kidney, the veins converge into from three to four great branches, which unite to form the renal, or emulgent vein. A preparation of all the vessels of the kidneys shows that the veins are much more voluminous than the arteries.

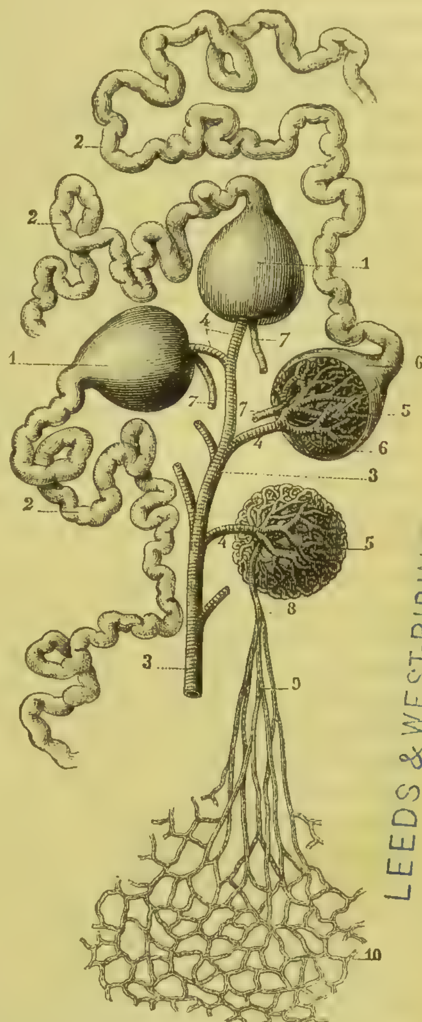


FIG. 116.—*Blood-vessels of the Malpighian bodies and convoluted tubes of the kidney.* (Sappey.) 1, 1, Malpighian bodies surrounded by the capsules of Müller; 2, 2, 2, convoluted tubes connected with the Malpighian body; 3, artery branching to go to the Malpighian bodies; 4, 4, 4, branches of the artery; 6, 6, Malpighian bodies from which a portion of the capsules has been removed; 7, 7, 7, vessels passing out of the Malpighian bodies; 8, vessel, the branches of which (9) pass to the capillary plexus (10).

The lymphatics of the kidney are few, and, according to Sappey, they only exist in the substance of the organ, converging toward the hilum. This author does not admit the existence of superficial lymphatics.

The nerves are quite numerous and are derived from the solar plexus, their filaments following the artery in its distribution in the interior of the organ and ramifying upon the walls of the vessels.

Mechanism of the Production and Discharge of Urine.

The striking peculiarities which the kidney presents in its structure, as compared with the true glands, and the fact of the voluntary discharge of its secretion at certain intervals, would naturally lead to a closer study of the mechanism of the production and discharge of the urine than we have given under the general head of the mechanism of the formation of the excretions. The composition of the urine, also, will be found to be exceedingly complex, and its various ingredients bear the closest relation to the processes of nutrition and disassimilation; all of which considerations render it of the greatest importance to ascertain the precise mode of its formation and to study all the conditions by which this process may be modified. In the present state of our knowledge, we must certainly regard the excrementitious constituents of the urine as formed essentially in the system at large, being merely separated from the blood by the kidneys; and a consideration of these effete principles belongs to the subject of nutrition. It remains for us, then, in this connection, to treat, in general terms, of the way in which these substances find their way into the urine.

The most important constituent of the urine is urea, a crystallizable, nitrogenized substance, which is discharged by the skin as well as by the kidneys. This has long been recognized as an excrementitious principle; but the first observations that gave any definite idea of the mechanism of its production were made by Prévost and Dumas, in 1821. At the time these experiments were made, chemists were not able to detect urea in the normal blood; but Prévost and Dumas extirpated the kidneys from living animals (dogs and cats), and found an abundance of urea in the blood, after certain symptoms of blood-poisoning had been manifested. The first experiments were performed by removing one kidney by an incision in the lumbar region, and, at the end of three or four days, after the animal had recovered from the first operation, removing the other. After the second operation, the animals lived for from five to nine days. For the first two or three days there were no symptoms of blood-poisoning. Watery discharges from the stomach and intestinal canal occurred after a few days, and finally stupor and other marked evidences of nervous disturbance supervened, when the presence of urea in the blood could be easily determined. These observations were confirmed and extended by Ségalas and Vauquelin, in 1822, who presented to the French Academy of Medicine a specimen of nitrate of urea extracted from the blood of a dog, taken sixty hours after extirpation of the kidneys, giving its proportion to the weight of blood employed. Since that time, as the processes for the determination of urea in the animal fluids have been improved, this substance has been detected in minute quantity in the normal blood. Picard carefully estimated and compared the proportions of urea in the renal artery and the renal vein, and he found that the quantity in the blood was diminished by about one-half in its passage through the kidneys. Still later, urea has been found by Wurtz to exist in the lymph and chyle in larger quantity, even, than in the blood. These facts, which have been almost universally regarded as established, have led physiologists to adopt the view that the peculiar excrementitious principles found in the urine are not produced by the kidneys, but are formed in the system by the general process of disassimilation, are taken up from the tissues by the blood, either directly or through the lymph, and are merely separated from the blood in the kidneys; and it has consequently been pretty generally assumed that nearly, if not all, the constituents of the urine preëxist in the circulating fluid. There is, indeed, no well-defined principle in the urine that has not been actually demonstrated in the blood. As an additional argument in favor of this view of the mechanism of urinary excretion, it has been ascertained that, when the kidneys are interrupted in their function, there is a tendency to the elimination of the excrementitious principles of the urine by the lungs, skin, and alimentary canal; and that these matters accumulate in the blood only after this vicarious effort has failed to effect their complete discharge. These ideas have seemed to be so completely justified by facts, that they have been applied to the mechanism of excretion by other organs, such as the skin and the liver; but, within a few years, the older observations with regard to nephrotomized animals have been discredited. It has been asserted, as the result of experiment, that urea and the urates do not accumulate in the blood after removal of the kidneys, and that this only occurs when both ureters have been tied. The experiments upon which this idea is based have been applied mainly to the pathology of uræmic intoxication, but it is evident that they bear directly upon the mechanism of excretion. It is not assumed, however, that excrementitious principles are not formed by the disassimilation of the tissues, but it is asserted that urea and the urates are produced in the kidneys by a transformation of excrementitious matters which exist in the blood.

The original experiments of Prévost and Dumas are very strong arguments in favor of the view that has been so long almost unquestioned, viz., that urea is simply separated from the blood by the kidneys; but the more recent observations of Bernard and Barreswil, Robin, and many others, while they confirm the first experiments on this subject, have added very considerably to our knowledge of the mechanism of uræmic poisoning after extirpation of the kidneys. The kidneys, it has been found, can readily be removed from living animals (dogs, cats, rabbits, etc.) without any great disturbance immediately following the operation. Bernard and Barreswil found that animals from which both kidneys had been removed did not usually present any distinctive symptoms for a day or two after, except that they vomited and passed an unusual quantity of liquid from the intestinal canal. During this period, the blood never contained an abnormal quantity of urea; but the contents of the stomach and intestine were found to be highly ammoniacal. During this time, also, the secretions from the stomach and intestines, particularly the stomach, became continuous, as well as increased in quantity. Animals operated upon in this way usually live for four or five days, and they then die in coma following upon convulsions. Toward the end of life, the secretion of gastric and intestinal fluids becomes arrested, probably from the irritating effects of ammoniacal decomposition of their contents, and then, and then only, urea is found to accumulate enormously in the blood.

It is thought by Bernard that the hypersecretion by the gastric and intestinal mucous membrane, in nephrotomized animals, is an effort on the part of the system to eliminate urea, which is decomposed by contact with these membranes into carbonate of ammonia. This view is sustained by the fact that, when urea is introduced into the alimentary canal in living animals, it disappears almost immediately and is replaced by the ammoniacal salts. Consequently, after removal of the kidneys, we should not expect to find an increased quantity of urea in the blood until its elimination by the mucous membrane of the alimentary canal has ceased; but the fact that it then accumulates in large quantity cannot be doubted.

The results obtained by other experimenters generally correspond with those of Bernard and Barreswil. It has also been ascertained, as was shown by Ségalas and Vauquelin, that urea is an active diuretic when injected in small quantity into the veins of a healthy animal; and that, in this case, it does not produce any poisonous effects, but is immediately eliminated. But, when urea is injected into the vascular system of a nephrotomized animal, it produces death in a very short time, with the characteristic symptoms of uræmic poisoning. We have frequently removed both kidneys from dogs, and, when the operation is carefully performed, the animals live for from three to five days. In some instances, they have been known to live for twelve days or even longer; but death always takes place finally with symptoms of blood-poisoning.

The experiments which are supposed to show that urea and the urates are actually formed in the kidneys, to which we have already alluded, were made with the view of comparing the effects of removal of both kidneys with those produced by tying the ureters. According to these observations, the blood contains much more urea after the ureters are tied than after removal of the kidneys. These experiments, which are directly opposed in their results to the well-considered observations of Prévost and Dumas, Bernard and Barreswil, Ségalas, and many others, cannot be accepted, unless it be certain that all the necessary physiological conditions have been fulfilled. In the first place, it was positively demonstrated, as early as 1847, that urea does not accumulate in the blood immediately after removal of the kidneys, but that this occurs only toward the end of life, and then urea is found in enormous quantity. In the second place, it is well known that the operation of tying the ureters is followed by an immense pressure of urine in the kidneys, which not only disturbs the eliminative action of these organs, but affects most seriously the general functions. Since the influence of the nervous system upon the secretions has been closely studied, it is evident that the pain and disturbance consequent upon the accumulation of urine above the ligated ureters must have an important reflex action upon the secretions; and this would probably interfere with the vicarious elimination of urea and other excrementitious principles by the stomach and intestines. It is well known to practical physicians that an arrest of these secretions, in cases of organic disease of the kidneys, is liable to be followed immediately by evidences of uræmia, and that grave uræmic symptoms are frequently relieved by the administration of remedies that act promptly and powerfully upon the intestinal canal. As an additional evidence of the great disturbance of the system—aside from the mere accumulation of excrementitious principles in the blood—which must result from tying the ureters, we have the intense distress and general prostration, always so prominent in cases of nephritic colic in which there may be merely temporary obstruction of one ureter.

From a careful review of the important facts bearing upon the question under consideration, there does not seem to be any valid ground for a change in our ideas concerning the mode of elimination of urea and the other important excrementitious constituents of the urine. There is every reason to suppose that these principles are produced in the various tissues and organs of the body during the process of disassimilation, are taken up by the blood, and are simply separated from the blood by the kidneys. There may be unimportant modifications of some of these principles in the kidneys or in the urine, such as the conversion of a certain amount of creatine into creatinine, but the great mass of excrementitious matter is separated from the blood by the kidneys unchanged.

Extirpation of one kidney from a living animal is not necessarily fatal. We have frequently performed this operation as a class-demonstration, and have kept the animal for weeks and months, without observing any indications of disturbance in the eliminative functions. If the operation be carefully performed, the wound will generally heal without difficulty, and in most instances the remaining kidney seems sufficient for the elimination of urine for an indefinite period. In all of our experiments, save one, the animals, killed long after the wound had healed, never presented any marked symptoms of retention of excrementitious matters in the blood. It is a noticeable fact, however, that in many instances they showed a marked change in disposition, and the appetite became voracious and unnatural. These animals would sometimes eat fæces, the flesh of dogs, etc., and, in short, presented certain of the phenomena so frequently observed after extirpation of the spleen. After extirpation of one kidney, it has been observed that the remaining kidney increases in weight, although recent investigations show that this is due mainly to an increase in the amount of blood, lymph, and urinary principles, and not to a new development of renal tissue. It is reasonable to suppose that Nature has provided, in the kidneys, more working substance than is ordinarily required for the elimination of the excrementitious constituents of the urine; and that, even when one kidney is removed, the other is competent to eliminate the amount of excrementitious matter that is produced, under ordinary conditions of the system. The exceptional experiment in which the animal died after extirpation of one kidney is quite interesting: October 6, 1864, we removed one kidney from a small cur-dog, about nine months old, by an incision in the lumbar region. The animal did not appear to suffer from the operation, and the wound healed kindly. The only marked effects were great irritability of disposition and an exaggerated and perverted appetite. He would attack the other dogs in the laboratory without provocation, and would eat with avidity, fæces, putrid dog's flesh, and articles which the other animals would not touch, and which he did not eat before the operation. On the morning of November 18th, forty-three days after the operation, the dog appeared to be uneasy, cried frequently, and at 12 o'clock went into convulsions, which continued until 3½ P. M., when he died. In one other instance, in which a dog was kept for more than a year after extirpation of one kidney, it was occasionally observed that the animal was rather quiet and indisposed to move for a day or two, but this always passed off, and when he was killed he was as well as before the operation.

Influence of the Nervous System, Blood-pressure, etc., upon the Secretion of Urine.—There are numerous instances in which very marked and sudden modifications in the action of the kidneys take place under the influence of fear, anxiety, hysteria, etc., when the impression must have been transmitted through the nervous system. Although little is known of the final distribution of the nerves in the kidney, it has been ascertained that here, as elsewhere, filaments from the sympathetic system ramify upon the walls of the blood-vessels, and they are undoubtedly capable of modifying the quantity and the pressure of blood in these organs.

It may be stated as a general proposition, that an increase in the pressure of blood in the kidneys increases the flow of urine, and that, when the blood-pressure is lowered, the flow of urine is correspondingly diminished. This fact will in a measure account for the increase in the flow of urine during digestion; but it cannot serve to explain all of the modifications that may take place in the action of the kidneys. The fact above stated, although it has been long recognized by physiologists, has lately been very fully illustrated by the experiments of Bernard. This observer measured the pressure of blood in the carotid artery of a dog and carefully noted the quantity of urine discharged in the course of a minute from one of the ureters. Afterward, by tying the two crural, the two brachial, and the two carotid arteries, he increased the blood-pressure about one-half, and the quantity of urine discharged in a minute was immediately increased by a little more than fifty per cent. In another animal, he diminished the pressure by taking blood from the jugular vein, and the quantity of urine was immediately reduced about one-half. His later observations on this subject showed that the increase in the quantity of urine produced by exaggerated pressure of blood in the kidneys was capable of being modified through the nervous system. In these experiments, the nerves going to one kidney were divided, which produced an increase in the arterial pressure and a consequent exaggeration in the quantity of urine from the ureter on that side. The pressure was then farther increased by stopping the nostrils of the animal. The quantity of urine was increased by this on the side on which the nerves had been divided, but the pain and distress from want of air arrested the secretion upon the sound side.

The precise influence which special nerves exert upon the secretion of urine has not yet been positively ascertained. Some important facts, however, bearing upon this subject have been developed of late years. In his interesting and novel experiments upon artificial diabetes in animals, Bernard found that, when irritation was applied to the floor of the fourth ventricle, in the median line, exactly in the middle of the space comprised between the origin of the pneumogastrics and the auditory nerves, the urine was increased in quantity and became strongly saccharine. When the irritation was applied a little above this point, the urine was simply increased in quantity, but it contained no sugar; and, when the puncture was made a little below, sugar appeared in the urine, without any increase in the quantity of the secretion. It has also been observed that section of the spinal cord in the upper part of the dorsal region arrests, for a time, the secretion of urine.

The final effect of division of all the nerves going to the kidney is very curious. The immediate effect of destruction of these nerves is to increase largely the amount of blood sent to the kidney, the organ then pulsating like an aneurismal tumor. In experiments upon this subject, by Müller and Peipers, the flow of urine was sometimes arrested by division of these nerves, but occasionally it continued. In these observations, the nerves were destroyed by applying a ligature tightly to the vessels as they enter at the hilum, including every thing but the ureter. The ligature was then loosened, so as to admit the blood, but the nerves had been bruised and destroyed. The secretion of urine continues, however, under these circumstances, for only a few hours. It then ceases, and the nutrition of the kidney becomes profoundly affected, its tissue breaking down into a putrid, semifluid mass, which probably enters the blood and is the cause of death.

The other physiological conditions that affect the urinary excretion influence the composition of the urine and the quantity of excrementitious matters separated by the kidneys. These will be more appropriately considered under the head of nutrition and disassimilation. It is sufficient to remark, in this connection, that, during digestion, when the composition of the blood is modified by the absorption of nutritive matters, the quantity of urine is usually increased. This is particularly marked when a large amount of liquid has been taken.

As the excrementitious principles eliminated by the kidneys are being constantly produced in the tissues by the process of disassimilation, the formation of urine is constant; presenting, in this regard, a marked contrast with the intermittent flow of most of the secretions proper, as distinguished from the excretions. It was noted by Erichsen, in a case of extroversion of the bladder, and it has been farther shown by experiments upon dogs, that there is an alternation in the action of the kidneys upon the two sides. Bernard exposed the ureters in a living animal and fixed a small silver tube in each, so that the secretion from each kidney could be readily observed; and he noted that a large quantity of fluid was discharged from one side for from fifteen to thirty minutes, while the flow from the other side was slight and in some instances was entirely arrested. The flow then commenced with activity upon the other side, while the discharge from the opposite ureter was diminished or arrested. We are already familiar with this alternation of action in the parotid glands.

Changes in the Composition of the Blood in passing through the Kidneys.—Some of the changes in the blood in its passage through the kidneys have already been noted. The most important of these consist in a diminution in the proportion of urea, the urates, and other of the excrementitious principles found in the urine. This would be expected, inasmuch as these principles are constantly present in the urine, and they have been shown to be derived exclusively from the blood. It has been ascertained, also, that the blood of the renal veins contains less water than the blood of any other part of the venous system. The constant separation of water from the blood by the kidneys, for the purpose of carrying off the soluble excrementitious principles, is an explanation of this fact. It was also observed by Simon, a number of years ago, that the blood of the renal veins does not coagulate readily, and that it is impossible to obtain fibrin from it in the ordinary way by stirring with rods.

Reference has already been made to the researches of Bernard, showing that the blood coming from many of the glands during their functional activity is but little darker than arterial blood. The action of the kidneys is constant, and the quantity of blood which they receive is enormous. Unless the function of these organs be disturbed, the blood passing through them cannot be deoxygenated, and it is consequently red, containing a large quantity of oxygen and a very small proportion of carbonic acid. This fact we have often noted, and it has been observed by all who have examined the renal veins in living animals. In comparative analyses for gases of the blood of the renal artery and vein, Bernard found, in one examination, no carbonic acid in either specimen, the proportion of oxygen being 12 parts per hundred in volume for the artery, and 10 parts for the vein. These observations were made at a temperature of from 50° to 53° Fahr. Making the analyses at about the temperature of the body (104° to 113°), the quantity of carbonic acid was 3 parts for the artery and 3·13 parts for the vein, and the proportion of oxygen was 19·46 parts for the artery and 17·26 parts for the vein. When the secretion of urine was arrested by irritation of the kidney, the blood became black in the vein, and the quantity of oxygen diminished, with a corresponding increase in the proportion of carbonic acid. These observations show that during secretion most of the blood sent to the kidneys is for the purpose of furnishing water and the excrementitious principles of the urine, and that but little is used for ordinary nutrition. Secretion appears to have no marked influence upon the consumption of oxygen and the production of carbonic acid.

Physiological Anatomy of the Urinary Passages.—The chief physiological interest attached to the anatomy of the urinary passages is connected with the discharge of the urine from the kidneys into the bladder, and with the process of micturition; and it will be necessary, consequently, to give but a brief account of the structure of these parts.

The excretory ducts of the kidneys (the ureters) commence each by a funnel-shaped sac, the pelvis, which is applied to the kidney at the hilum. This sac presents little tubular processes, called calices, into which the apices of the pyramids are received. The ureters themselves are membranous tubes of about the diameter of a goose-quill, becoming much reduced in caliber as they penetrate the coats of the bladder. They are from sixteen to eighteen inches in length, passing from the kidneys to the bladder behind the peritoneum. They have three distinct coats: an external coat, composed of fibrous tissue, the ordinary white fibres mixed with elastic fibres of the small variety; a middle coat, composed of different layers of non-striated muscular fibres; and a mucous coat.

The external coat requires no special description. It is prolonged into the calices and is continuous with the fibrous coat of the kidney at the apices of the pyramids.

The fibres of the muscular coat present two principal layers; an external longitudinal layer, and an internal transverse, or circular layer, to which is added near the bladder a layer of longitudinal fibres, internal to the circular fibres.

The mucous lining is thin, smooth, and without any follicular glands. It is thrown into slight longitudinal folds, when the tube is flaccid, which are easily effaced by distention. The epithelium exists in several layers and is remarkable for the irregular shape of the cells. They present, usually, numerous dark granulations and one or two clear nuclei with distinct nucleoli. Some of the cells are flattened, some are rounded, and some are caudate, with one or two prolongations.

Passing to the base of the bladder, the ureters become constricted, penetrate the coats of this organ obliquely, their course in its walls being a little less than an inch in length. This valvular opening allows the free passage of the urine from the ureters, but compression or distention of the bladder closes the orifices and renders a return of the fluid impossible.

The bladder, which serves as a reservoir for the urine, varies in its relations to the pelvic and abdominal organs as it is empty or more or less distended. When perfectly empty, it lies deeply in the pelvic cavity and is then a small sac, of an irregularly triangular form. As it becomes filled, it assumes a globular or ovoid form, rises up in the pelvic cavity, and, when excessively distended, it may project into the abdomen. When the urine is voided at normal intervals, the bladder, when filled, contains about a pint of liquid; but, under pathological conditions, it may become distended so as to contain ten or twelve pints, and, in some instances of obstruction, it has been found to contain even more. The bladder is usually more capacious in the female than in the male. It is held in place by certain ligaments and folds of the peritoneum, which it is unnecessary to describe in this connection, but which are so arranged as to allow of the various changes in volume and position which the organ is liable to assume under different degrees of distention.

The anatomy of the coats of the bladder possesses a certain amount of physiological interest. These are three in number. The external coat is simply a reflection of the peritoneum, covering the posterior portion completely, from the openings of the ureters to the summit, about one-third of the lateral portion, and a small part of the anterior portion.

The middle, or muscular coat, consists of fibres of the non-striated or involuntary variety, arranged in three tolerably distinct layers.

The external muscular layer is composed of longitudinal fibres, which arise from parts adjacent to the neck, and pass anteriorly, posteriorly, and laterally over the organ, so that when they are contracted they diminish its capacity chiefly by shortening its vertical diameter. The anterior fibres of this layer arise from the body of the pubis and the symphysis, by tendinous bands, known to most anatomists as the anterior ligaments. These tendinous fibres spread out upon the prostate and are attached to its anterior surface. As the fibres on the anterior surface pass over the summit of the bladder, they interlace, and some of them are continuous with the fibres coming from the posterior surface. The posterior fibres arise from the base of the prostate, and, after forming a distinct band an inch or an inch and a quarter in breadth, spread out upon the posterior surface of the bladder. The lateral fibres arise from the sides of the prostate and spread out upon the lateral surfaces of the bladder. In the female, the posterior fibres arise from the dense fibrous membrane between the neck of the bladder and the vagina, and the lateral fibres, from the perineal aponeurosis, the anterior fibres arising from the pubis, as in the male. The fibres of the external layer are of a pinkish hue, being much more highly colored than the other layers.

The middle muscular layer is formed of circular fibres, arranged, on the anterior surface of the bladder, in distinct bands at right angles to the superficial fibres. They are thinner and less strongly marked on the posterior and lateral surfaces.

The internal muscular layer is composed of excessively pale fibres arranged in longitudinal fasciculi, the anterior and lateral bundles anastomosing with each other as they descend toward the neck of the bladder, by oblique bands of communication, and the posterior bundles interlacing in every direction, forming an irregular plexus. Here they are not to be distinguished from the fibres of the middle layer. This arrangement has given to these fibres the name of the plexiform layer, and it gives to the interior of the bladder its reticulated appearance. This layer is continuous with the muscular fibres of the urachus, the ureters, and the urethra.

The sphincter vesicæ is composed of a band of smooth fibres, about half an inch in breadth and one-eighth of an inch in thickness, embracing the neck of the bladder and the posterior half of the prostatic portion of the urethra. The tonic contraction of these fibres prevents the flow of urine, and, during the ejaculation of the seminal fluid, it offers an obstruction to its passage into the bladder.

It is seen, from the arrangement of the muscular fibres of the bladder, that they are capable by their contraction of expelling the greatest part of the urine when the sphincter is relaxed.

The mucous membrane of the bladder is smooth, rather pale, thick, and loosely adherent to the submucous tissue, except over the corpus trigonum. The epithelium exists in several layers and presents the same diversity in form as that observed in the pelvis of the kidney and the ureters; viz., the deeper cells are elongated and resemble the columnar epithelium, while the cells on the surface are flattened. In the neck and fundus of the bladder are a few mucous glands, some in the form of simple follicles, and others collected to form glands of the simple racemose variety.

The corpus trigonum is a triangular body, lying just beneath the mucous membrane at the base of the bladder and extending from the urethra in front to the openings of the ureters. It is composed of white fibrous tissue, with a few elastic and muscular fibres. At the opening of the urethra, it presents a small projecting fold of mucous membrane, which is sometimes called the uvula vesicæ. Over the whole of the surface of the trigone, the mucous membrane is very closely adherent, and it is never thrown into folds, even when the bladder is entirely empty.

The blood-vessels going to the bladder are ultimately distributed to its mucous membrane. They are not very numerous, except at the fundus, where the mucous membrane is tolerably vascular. Lymphatics have been described as existing in the walls of the bladder, but Sappey, whose researches in the lymphatic system have been very extended and successful, has failed to demonstrate them in this situation. The nerves of the bladder are derived from the hypogastric plexus.

The urethra is provided with muscular fibres, and it is lined by a mucous membrane, the anatomy of which will be more fully considered in connection with the function of generation. In the female the epithelium of the urethra is like that of the bladder. In the male the epithelial cells are small, pale, and of the columnar variety.

Mechanism of the Discharge of Urine.—In some of the lower orders of animals in which the urine is of a semisolid consistence, the movement of vibratile cilia in the uriniferous tubes probably aids in the discharge of the excretion; but, in the human subject, the existence, even, of cilia is doubtful, and the urine is discharged into the pelves of the kidneys and the ureters by pressure due to the act of separation of the fluid from the blood. Once discharged into the ureters, the course of the urine is determined in part by the *vis a tergo*, and in part, probably, by the action of the muscular coats of these canals. Müller has found that the ureters can be made to undergo a powerful local contraction upon the application of a galvanic current; and Bernard has shown that this may be produced by galvanization of the anterior root of the eleventh dorsal nerve. Notwithstanding these facts, it is difficult to estimate the amount of influence ordinarily exerted by peristaltic contractions of the ureters; but, when there is excessive accumulation of urine in the bladder, or when there is obstruction from any cause, such as the presence of a renal calculus, these contractions are probably quite energetic.

When the urine has accumulated to a certain extent in the bladder, a peculiar sensation is experienced which leads to the act for its expulsion. This desire to discharge the urine is probably due to the impression produced by the distention of the bladder. The intervals at which it is experienced are exceedingly variable. The urine is usually voided before retiring to rest and upon rising in the morning, and generally two or three times, in addition, during the day. The frequency of micturition, however, depends very much upon habit, upon the quantity of liquids ingested, and upon the degree of activity of the skin; the latter conditions modifying the quantity of urine.

Evacuation of the bladder is accomplished by the muscular walls of the organ itself, aided by contractions of the diaphragm and the abdominal muscles with certain muscles which operate upon the urethra, and it is accompanied by relaxation of the sphincter vesicæ. This act is at first voluntary, but, once commenced, it may be continued by the involuntary contraction of the bladder alone. During the first part of the process, the distended bladder is compressed by contraction of the diaphragm and the abdominal muscles; and this, after a time, excites the action of the bladder itself. A certain period usually elapses then before the urine begins to flow. When the bladder contracts, aided by the muscles of the abdomen and the diaphragm, the resistance of the sphincter is overcome, and a jet of urine flows with considerable force from the urethra. All voluntary action may then cease for a time, and the bladder will nearly empty itself; but the force of the jet may at any time be considerably increased by voluntary effort.

It is a question whether the bladder be capable of entirely emptying itself by the action of its muscular walls. That almost all the urine may be expelled in this way in the human subject, there can be no doubt; and it has been shown by experiments upon some of the inferior animals that the bladder may be completely evacuated when it has been drawn out of the abdominal cavity. In vivisections, we have frequently observed the bladder so firmly contracted that it could contain hardly more than a few drops of liquid.

Toward the end of the expulsive act, when the quantity of liquid remaining in the bladder is slight, the diaphragm and the abdominal muscles are again called into action, and there is a convulsive, interrupted discharge of the small quantity of urine that remains. At this time, the impulse from the bladder, and, indeed, the influence of the abdominal muscles and diaphragm, are very slight, and the flow of urine along the urethra is aided by the contractions of its muscular walls and the action of some of the perineal muscles, the most efficient being the accelerator urinæ; but with all this muscular action a few drops of urine generally remain in the male urethra after the act of urination is accomplished. The process of evacuation of urine in the female is essentially the same as in the male, with the exception of the slight modifications due to differences in the direction and length of the urethra.

The movements of the bladder are under the control of the nervous system. According to the researches of Budge, the influence of the nervous system operates through the sympathetic, and he has described a centre in the spinal cord, which presides over the contractions of the lower part of the intestinal canal, the bladder, and the vasa deferentia. This he calls the genito-spinal centre, and he has located it, in experiments upon rabbits, in the spinal cord, at a point opposite the fourth lumbar vertebra. From this centre, the nervous filaments pass through the sympathetic nerve communicating with the ganglion which corresponds to the fifth lumbar vertebra.

Properties and Composition of the Urine.

The importance of an exact knowledge of the properties and composition of the urine has long been recognized by physiologists; and our literature is full of observations, more or less valuable, upon this subject, dating from the discovery of urea, by Hillaire Rouelle, in the latter part of the last century, to the present time. It is impossible, however, to follow out in detail even the most important of the chemical researches upon the different urinary constituents, without exceeding the limits of pure human physiology; and the observations of the earlier authors have now little more than an historical interest. But this can hardly be said of the analysis of the urine by Berzelius, made early in the present century; for, even in recent authoritative works upon physiology, these are quoted as the most elaborate and reliable of the quantitative examinations of the renal excretion. In treating of this subject, we propose to give simply the chemistry of the urine as it is understood at the present day, dwelling particularly upon its relations to the physiology of nutrition and disassimilation. In doing this it will be necessary to consider carefully the quantity, specific gravity, reaction, etc., of the urine, with the variations observed under different physiological conditions.

General Physical Properties of the Urine.—The color of the urine is very variable within the limits of health, and it depends to a considerable extent upon the character of the food, the quantity of drink, and the activity of the skin. As a rule, the color is yellowish or amber, with more or less of a reddish tint. The fluid is perfectly transparent, free from viscidity, and exhales, when first passed, a peculiar, aromatic odor, which is by no means disagreeable. Soon after the urine cools, it loses this peculiar odor and has the odor known as urinous. This odor remains until the liquid begins to undergo decomposition. The color and odor of the urine are usually modified by the same physiological conditions. When the fluid contains a relatively large amount of solid matters, the color is more intense and the urinous odor is more penetrating; and, when its quantity is increased by an excess of water, the specific gravity is low, the color pale, and the odor faint. The urine passed in the morning is usually more intense in color than that passed during the day.

It is somewhat difficult to measure the exact temperature of the urine at the moment of its emission. In the observations on this subject, by Dr. Byasson, in which a very delicate thermometer was used and extraordinary care was taken to prevent any change in temperature before the estimate was made, the temperature, under physiological conditions, varied but a small fraction of a degree from 100° Fahr. It is important to know the normal temperature of the urine, as it is liable to vary very considerably in certain diseases.

Quantity, Specific Gravity, and Reaction of the Urine.—In estimating the total quantity of urine discharged in the twenty-four hours, it is important to take into consideration the specific gravity, as an indication of the amount of solid matter excreted by the kidneys. We have already alluded to some of the variations in quantity constantly occurring in health, as depending upon the proportion of water; but the amount of solid matters excreted is usually more nearly uniform. It must also be taken into account that differences in climate, habits of life, etc., in different countries, have an important influence upon the daily quantity of urine. Dr. Parkes has collected the results of twenty-six series of observations made in America, England, France, and Germany, and he finds the average daily quantity of urine in healthy male adults, between twenty and forty years of age, to be fifty-two and a half fluidounces, the average quantity per hour being two and one-tenth fluidounces. The extremes were thirty-five and eighty-one ounces.

In attempting to decide the question whether a certain quantity of urine passed be abnormal or within the limits of health, it is important to recognize, if possible, certain limits of physiological variation. Becquerel states that the variations in the proportion of water in the urine likely to occur in health are between twenty-seven and fifty fluidounces; but his average of the total quantity in the twenty-four hours is only forty-four ounces, which is rather lower than the one we are disposed to adopt. The circumstances that lead to a diminution in the proportion of water are usually more efficient in their operation than those which tend to an increase; and the range below the healthy standard is rather wider than it is above. All these estimates, however, are merely approximative. Assuming that the usual quantity in the male is about fifty ounces, it may be stated, in general terms, that the range of normal variation is between thirty and sixty; and that, when the quantity varies much from these figures, it is probably due to some pathological condition.

According to the researches of Becquerel, the quantity of water discharged by the kidneys in the twenty-four hours is a little greater in the female than in the male; but in the female the specific gravity is lower, and the amount of solid constituents is relatively and absolutely less.

The specific gravity of the urine should always be estimated in connection with the absolute quantity in the twenty-four hours. Those who assume that the daily quantity is about fifty ounces give the ordinary specific gravity of the mixed urine of the twenty-four hours, at 60° Fahr., as about 1020. The specific gravity is liable to the same variations as the proportion of water, and the density is increased precisely as the amount of water is diminished. The ordinary range of variation in specific gravity is between 1015 and 1025; but, without positively indicating any pathological condition, it may be as low as 1005 or as high as 1030.

The reaction of the urine is acid in the carnivora and alkaline in the herbivora. In the human subject, it is usually acid at the moment of its discharge from the bladder; although at certain periods of the day it may be neutral or feebly alkaline, the reaction depending upon the character of the food. The acidity may be measured by carefully neutralizing the urine with an alkali, in a solution that has previously been graduated with a solution of oxalic acid of known strength; and the degree of acidity is usually expressed by calling it equivalent to so many grains of crystallized oxalic acid.

As the result of numerous observations made by Vogel and under his direction, the total quantity of acid in the urine of the twenty-four hours in a healthy adult male is equal to from two to four grammes, or, omitting fractions, to from thirty to sixty grains of oxalic acid. The hourly quantity in these observations was equal, in round numbers, to from one and a half to three grains of acid. The proportion of acid was found to be very variable in the same person at different periods of the day. In one individual, upon whom the greatest number of observations was made, the average hourly quantity of acid at night was 2·9 grains; in the forenoon, 2 grains; and in the afternoon, 2·3 grains. "In a series of experiments made upon four different persons, the quantity was found to be greatest at night, least in the forenoon, and between these extremes in the afternoon."

In estimating the degree of acidity of the urine, it is necessary to test the fluid as soon as possible after it is discharged from the bladder; for its acidity rapidly increases after emission—until ammoniacal decomposition sets in—by the formation of organic acids, particularly the lactic.

There has been considerable discussion and difference of opinion among physiological chemists with regard to the cause of the acid reaction of the urine. At the moment of its discharge from the bladder, it is distinctly and even strongly acid; but it will not decompose the carbonates, like most acid solutions. The weight of chemical authority upon this point is in favor of the view that there is no free acid in the urine when it is first passed, although the lactic acid, the acid lactates, and, perhaps, some other of the organic acids may be produced after emission, as the result of decomposition; but nearly all authors agree that it contains the acid phosphate of soda. The phosphates exist in the fluids of the body in at least three different conditions. The basic phosphate of soda, for example, possesses three atoms of the base and has an alkaline reaction. In contact with carbonic acid, this salt may lose one atom of the base, forming the carbonate of soda and what is called the neutral phosphate, the latter, however, having a feebly alkaline reaction. In contact with uric acid, the neutral phosphate may lose still another atom of base, forming the urate of soda and the acid phosphate; and, according to most authorities, it is in this form that it exists in the urine, and the presence of this salt is the cause of its acidity. The acid phosphate of soda may or may not be associated, in the human subject, with the acid phosphate of lime, which ordinarily gives the intensely acid reaction to the urine of the carnivora.

Composition of the Urine.

Regarding the excrementitious constituents of the urine as a measure, to a certain extent, of the general process of disassimilation, it is probably more important to recognize the absolute quantity of these principles discharged in a definite time than to learn simply their proportions in the urine; and, in making out a table of the composition of the urine, we shall give, as far as possible, the absolute quantity of its different constituents excreted in twenty-four hours. This latter point, however, will be more elaborately considered in connection with the characters of the individual excrementitious principles and their variations under physiological conditions. In compiling this table, we have taken advantage of the elaborate bibliographical and experimental researches of Prof. Robin, contained in his recent work upon the humors,[1] but we have ventured to make some changes and corrections in his list of urinary constituents:

[1] Robin, *Leçons sur les humeurs*, Paris, 1874. In the table given by Robin (p. 762), there is evidently a very serious error in one of the figures giving the proportion of water and an error in the proportion of oxygen. We have omitted some of the constituents given by Robin, which are stated to be doubtful or accidental, or are noted as present under pathological conditions.

Although the table represents, very nearly, the latest and most reliable observations upon the relative and absolute quantities of the urinary constituents, there are a few minor points that demand some explanation. For example, Robin estimates the proportion of hippurates at a little less than the proportion of urates, while many writers of high authority speak of the hippurates as excreted in rather larger quantity; but the investigations with regard to the daily excretion of hippuric acid have not been so definite and satisfactory as those upon which the estimates of the excretion of uric acid are based. Robin gives, also, the proportion of creatine as 1·4 to 2·6 parts per 1,000, and of creatinine, 0·2 to 0·4 per 1,000; and most authors give in the urine a larger proportion of creatinine. This difference, however, is not important, for, as far as the process of excretion is concerned, these two substances may be regarded as a single principle, creatine being readily converted into creatinine in the urine by simple decomposition. In our endeavor to make this table as complete as possible, we have reduced the figures given by many authors to represent the amounts of uric acid, phosphoric acid, sulphuric acid, chlorine, etc., to the quantity of the salts as they actually exist. This is particularly important in a work on physiology, for chlorine and the various acids just enumerated are not proximate constituents of the urine, except when combined with bases. It is simply a matter of convenience to estimate them separately, and the proportions of salts are readily calculated from the combining equivalents of the different elements.

Composition of the Human Urine.

Water (in 24 hours, 27 to 50 fluidounces—Becquerel)		967·47 to	940·36
Urea (in 24 hours, 355 to 463 grains—Robin)		15·00 "	23·00
Uric acid, accidental, or traces			
Urate of soda, neutral and acid	(In 24 hours, 6 to 9 grs. of uric acid—Becquerel—or 9 to 14 grs. of urates, estimated as neut. urate of soda.)	1·00 "	1·60
Urate of ammonia, neutral and acid (in small quantity)			
Urate of potassa			
Urate of lime			
Urate of magnesia			
Hippurate of soda	(In 24 hours, about 7·5 grs. of hippuric acid—Thudichum—equivalent to about 8·7 grs. of hippurate of soda.)	1·00 "	1·40
Hippurate of potassa			
Hippurate of lime			
Lactate of soda	(Daily quantity not estimated)	1·50 "	2·60
Lactate of potassa			
Lactate of lime			
Creatine	(In 24 hours, about 11·5 grains of both—Thudichum)	1·60 "	3·00
Creatinine			
Oxalate of lime (daily quantity not estimated)		traces "	1·10
Xanthine		not estimated.	
Margarine, oleine, and other fatty matters		0·10 to	0·20
Chloride of sodium (in 24 hours, about 154 grains—Robin)		3·00 "	8·00
Chloride of potassium		traces.	
Hydrochlorate of ammonia		1·50 to	2·20
Sulphate of soda	(In 24 hours, 23 to 38 grains of sulphuric acid—Thudichum. About equal parts of sulphate of soda and sulphate of potassa—Robin—equivalent to from 22·5 to 37·5 grains of each.)	3·00 "	7·00
Sulphate of potassa			
Sulphate of lime (traces)			
Phosphate of soda, neutral	(Daily quantity not estimated)	2·50 "	4·30
Phosphate of soda, acid			
Phosphate of magnesia (in 24 hours, 7·7 to 11·8 grains—Neubauer)		0·50 "	1·00
Phosphate of lime, acid	(In 24 hours, 4·7 to 5·7 grains—Neubauer)	0·20 "	1·30
Phosphate of lime, basic			
Ammonio-magnesian phosphate (daily quantity not estimated)		1·50 "	2·40
(Daily excretion of phosphoric acid, about 56 grains—Thudichum.)			
Silicic acid		0·03 "	0·04
Urrosacine		0·10 "	0·50
Mucus from the bladder			
		1,000·00	1,000·00

Proportion of solid constituents, from 32·63 to 59·89 parts per 1,000.

Gases of the Urine. (Parts per 1,000, in volume.)

Oxygen, in solution	0·90 "	1·00
Nitrogen, in solution	7·00 "	10·00
Carbonic acid, in solution	45 "	50·00

Urea.—As regards quantity, and probably as a measure of the activity of the general process of disassimilation, urea is the most important of the urinary constituents; and this substance, with the changes which it undergoes in the urine and the mode of its production in the system, has been most carefully studied by physiologists. Regarding the daily excretion of urea as a measure of nutritive force and physiological waste, its consideration would come properly under the head of nutrition, in connection with all other substances known to be the results of disassimilation; but it is more convenient to treat of its general physiological properties, and some of its variations in common with other excrementitious principles separated by the kidneys, in connection with the composition of the urine.

The formula for urea, showing the presence of a large proportion of nitrogen, would lead us to suppose that this substance is one of the products of the waste of the nitrogenized principles of the body. It is found, under normal conditions, in the urine, the lymph and chyle, the blood, the sweat, and the vitreous humor. Its presence has lately been demonstrated, also, in the substance of the healthy liver in both carnivorous and herbivorous animals; and it has farther been shown by Zalesky that it exists in minute quantity in the muscular juice. Under pathological conditions, as has been already intimated, urea finds its way into various other fluids, such as the secretion from the stomach, the serous fluids, etc.

In connection with the chemical properties of urea, it is interesting to note that it is one of the few organic proximate principles that can be produced synthetically in the laboratory of the chemist. As early as 1828, Wöhler obtained urea by adding sulphate of ammonia to a solution of cyanate of potassa. The products of this combination are sulphate of potassa, with cyanic acid and ammonia in a form to constitute urea. The cyanate of ammonia is isomeric with urea, and the change is effected by a simple rearrangement of its elements. It has long been known that urea, in contact with certain animal substances, is readily convertible into carbonate of ammonia. This transformation is theoretically accomplished by adding to urea four atoms of water. It has recently been stated by Kolbe, that carbonate of ammonia, when heated in sealed tubes to the temperature at which urea commences to decompose, is converted into urea. The decomposition of urea resulting in the carbonate of ammonia may be easily effected by various chemical means. As this occurs in the spontaneous decomposition of urea in the urine and elsewhere, it has been supposed that the symptoms of blood-poisoning following retention of the urinary constituents, in cases of disease of the kidneys, are due to the decomposition of the urea into carbonate of ammonia, and not to the presence of the urea itself in the blood. Many interesting experiments and observations have been made upon this subject, but it is now pretty generally admitted that the weight of evidence is against the carbonate-of-ammonia theory of uræmia.

Except as regards the probable changes that take place in the process of transformation of certain constituents of the tissues into urea, the chemical history of this substance does not present much physiological interest. Urea may be readily extracted from the urine, by processes fully described in all the modern works upon physiological chemistry; and its proportion may now be easily estimated by the new methods of volumetric analysis. It is not so easy, however, to separate it from the blood or the substance of any of the tissues, on account of the difficulty in getting rid of the other organic matters and the great facility with which it undergoes decomposition.

Fig. 117.—*Urea, crystallized from an aqueous solution.* (Funke.)

When perfectly pure, urea crystallizes in the form of long, four-sided, colorless, and transparent prisms, which are without odor, neutral, and in taste resemble saltpetre. These crystals are very soluble in water and in alcohol, but they are entirely insoluble in ether. In its behavior to reagents, urea acts as a base, combining readily with certain acids, particularly nitric and oxalic. It also forms combinations with certain salts, such as the oxide of mercury, chloride of sodium, etc. It exists in the economy in a state of watery solution, with perhaps a small portion of it modified by the presence of chloride of sodium.

Origin of Urea.—There are two probable sources of urea in the economy, assuming that it always preëxists in the blood and is not formed in the kidneys. One of these is in the disassimilation of the nitrogenized constituents of the tissues, and the other, in a transformation in the blood of an excess of the nitrogenized elements of food. Urea, as we have already seen, exists in considerable quantity in the lymph and chyle, and it is found, also, in small proportion, in the blood. It has lately been detected in still smaller quantity in the muscular tissue; but chemists have thus far been unable to extract it from any other of the solid tissues, under normal conditions, except the substance of the liver. The fact that it exists in considerable quantity in the liver has led to the supposition that this is the organ chiefly concerned in its production. With the small amount of positive information that we have upon this point, the view that the liver produces urea, while the kidneys are the organs chiefly concerned in its elimination, must be regarded as purely hypothetical. But, if it be true that urea is the result of the physiological wear of the nitrogenized elements of the body, the liver would probably produce its share, in the ordinary process of disassimilation. The fact that urea has not yet been detected in normal muscular tissue is by no means a conclusive argument against its formation in this situation. We have lately shown that, although the liver is constantly producing sugar, none can be detected in its substance, for the reason that it is washed out as fast as it is formed, by the current of blood. In the case of the muscles, it is by no means improbable that the lymph, and perhaps the blood, wash out the urea constantly and keep these parts free from its presence during normal conditions. In some late experiments by Meissner, in which the observations of Prévost and Dumas on the accumulation of urea in the blood of nephrotomized animals were confirmed, urea was found in dogs and rabbits, after removal of the kidneys, not only in the liver but in the muscles and brain.

Although our experimental knowledge does not warrant the unreserved conclusion that urea is produced primarily in the nitrogenized parts of the organism, particularly the muscular tissue, this view is exceedingly probable; and we must wait for farther information on this subject, until physiological chemists are able to follow out more closely the exact atomic changes that intervene between the functional operation of organized parts and the change of their substance into excrementitious matters.

When we come to consider the influence of food upon the composition of the urine, it will be seen that an excess of nitrogenized matter taken into the alimentary canal causes a proportionate increase in the quantity of urea discharged. This fact has led to the supposition that a part of the urea contained in the urine is the result of a direct transformation in the blood of the nitrogenized alimentary principles. This view must be regarded as purely hypothetical. We do not even know the nature of the process by which the nitrogenized elements of the tissues are transformed into excrementitious matter, and we are still more ignorant of the essential characters of nutrition proper. When more nitrogenized food is taken than is absolutely necessary, it is evident that the excess must be discharged from the system. This is never discharged in the form in which it enters, like an excess of chloride of sodium or other inorganic matter, but it is well known that a series of complicated changes are necessary, even before organic matters can be taken into the blood by absorption. There is no evidence of the direct transformation of these principles into urea before they have become part of the organized structures, except in a comparison of the proportions of nitrogen ingested and discharged; and this proves nothing with regard to the nature of the intermediate processes. At the present time, the most rational supposition is, that the nitrogenized elements of food nourish the corresponding constituents of the body, which are constantly undergoing conversion into excrementitious matters. Observations which have appeared to demonstrate the formation of urea directly from albuminoid substances have not been confirmed.

There are certain arguments, based upon comparisons of the atomic constitution of urea with the elements of uric acid, creatine, and creatinine, in favor of the view that urea is the product of a higher degree of oxidation of the other excrementitious matters above mentioned. It has been found, also, that urea may be formed artificially from uric acid, creatine, creatinine, xanthine, hypoxanthine, and some other bodies of similar nature. That certain bodies are mutally convertible by the addition or subtraction of a few elements of water, there can be no doubt. Examples of these simple transformations are, the change of starch, dextrine, etc., into glucose, the change of creatine into creatinine, etc., but the atomic changes necessary for the conversion into urea of the principles from which this substance has been assumed to be produced are much more complicated. There is no positive proof that the proportion of these various principles in the muscles, blood, and urine, bears an inverse ratio to the proportion of urea. Again, the argument that the excrements of reptiles contain an excess of uric acid because the activity of oxidation is less than in the mammalia is met by the fact that, in birds, in which the amount of oxygen consumed is greater, the proportion of urates is enormous; and urea is not generally found in this class, but is contained only in the excrements of the rapacious birds, and here only in small quantity.

There are no sufficient reasons for regarding urea as the final result of oxidation of certain of the tissues of the body, uric acid, creatine, etc., being substances in an intermediate stage of transformation; and we are forced to admit that this principle is formed during the general process of disassimilation, probably from the nitrogenized elements of the body, by a destructive action, with the exact nature of which we are as yet imperfectly acquainted.

The daily amount of urea excreted is subject to very great variations. It is given in the table as ranging between 355 and 463 grains. This is much less than the estimates frequently given; but, when the quantity has been very large, it has generally depended upon an unusual amount of exercise or of nitrogenized food, or the weight of the body has been above the average. Parkes gives the results of twenty-five different series of observations upon this point. The lowest estimate is 286·1 grains, and the highest, 688·4 grains.

Uric Acid and its Compounds.—Uric acid seldom if ever exists in a free state in normal urine. It is exceedingly insoluble, requiring from fourteen to fifteen thousand times its volume of cold water, and from eighteen to nineteen hundred parts of boiling water for its solution. It was at one time supposed to exist in the urine in sufficient quantity to give it its acid reaction; but it has since been ascertained that its solution does not redden litmus. Its presence in the urine uncombined must be regarded as a pathological condition; still, it is often found in urinary deposits, where it is interesting to study the peculiar and varied forms of its crystals. Frequently, in tables of the composition of the urine, the proportion of uric acid is given, but this is simply a matter of convenience, and it has precisely the same signification as the estimates of the proportions of sulphuric or of phosphoric acid. None of these acids constitute, of themselves, proximate principles of the urine, but they are always combined with bases.

In normal urine, uric acid is combined with soda, ammonia, potassa, lime, and magnesia. Of these combinations, the urate of soda and the urate of ammonia are by far the most important and constitute the great proportion of the urates, the urates of potassa, lime, and magnesia existing only in minute traces. The urate of soda is very much more abundant than the urate of ammonia. The union of uric acid with the bases is very feeble. If from any cause the urine become excessively acid after its emission, a deposit of uric acid is liable to occur. The addition of a very small quantity of almost any acid is sufficient to decompose the urates, when the uric acid appears, after a few hours, in a crystalline form.

Uric acid, probably in combination with bases, was found in the substance of the liver in large quantity by Cloetta, and his observations have been confirmed by recent German authorities. It is more than probable that the urates also exist in the blood and pass ready-formed into the urine; but their proportion in the blood is so slight, under normal conditions, that their presence in this fluid has not been definitely determined, except in birds, in which Meissner has lately found it in considerable quantity. The fact that the urates exist in the liver, and in no other part—except, perhaps, the spleen—has led Meissner to the opinion that this organ is the principal seat of the formation of uric acid. However this may be—and the facts do not seem sufficiently definite to lead to such an exclusive opinion—it is certainly not formed in the kidneys, but is simply separated by these organs from the blood. Meissner did not succeed in finding uric acid in the muscular tissue, although the specimens were taken from the same animals in which he had found large quantities in the liver.

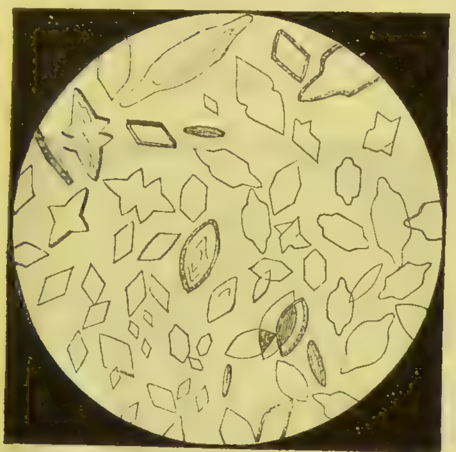


Fig. 118.—*Crystals of uric acid obtained partly by the solution and subsequent precipitation of chemically pure acid, and partly by decomposition of the urates by nitric or acetic acid.* (Funke.)

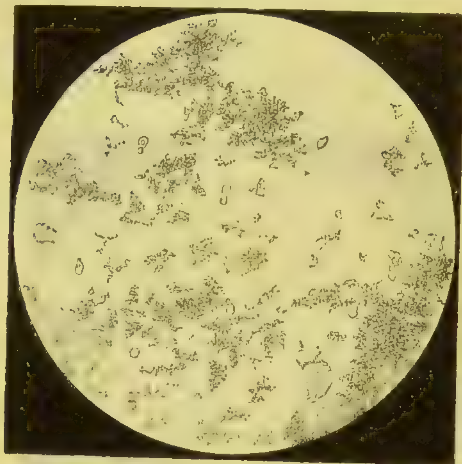


Fig. 119.—*Urate of soda.* (Funke.)

We have already discussed the theory of the change of uric acid into urea. In the present state of our knowledge, we must regard the urates, particularly the urate of soda, as among the products of disassimilation of the nitrogonized constituents of the body; and we should admit that as yet we are unable to designate the precise seat of their formation or to follow out all the processes involved in their production.

The daily excretion of uric acid, given in the table, is from six to nine grains; which is equal to from nine to fourteen grains of urates estimated as neutral urate of soda. Like urea, the proportion of the urates in the urine is subject to certain physiological variations, which will be considered farther on.

Hippuric Acid, Hippurates, and Lactates.—The compounds of hippuric acid, which are so abundant in the urine of the herbivora, are now known to be constant constituents of the human urine. Hippuric acid is always to be found in the urine of children, but it is sometimes absent temporarily in the adult. The hippurates have been detected in the blood of the ox by Verdeil and Dolfuss, and they have since been found in the blood of the human subject. There can be scarcely any doubt that they pass, ready-formed, from the blood into the urine. With regard to the exact mode of origin of the hippurates, we have even less information than upon the origin of the other urinary constituents already considered. Experiments have shown that the proportion of hippuric acid in the urine is greatest after taking vegetable food; but it is found after a purely animal diet, and probably it also exists during fasting. We must be content at present simply to class the hippurates among the products of disassimilation, without attempting to specify their exact mode of origin. The daily excretion of hippuric acid amounts to about 7·5 grains, which is equivalent to about 8·7 grains of hippurate of soda.

Hippuric acid itself, unlike uric acid, is quite soluble in water and in a mixture of hydrochloric acid. It requires six hundred parts of cold water for its solution, and a much smaller proportion of warm water. Under pathological conditions, it is sometimes found free in solution in the urine.

The lactates of soda, potassa, and lime, exist in very considerable proportion in the normal urine. They are undoubtedly derived immediately from the blood, passing ready-formed into the urine, where they exist in simple watery solution. According to Robin, the lactates are formed in the muscles, in the substance of which they can be readily detected. We have no positive information with regard to the precise mode of formation of these salts. It is probable, however, that the lactic acid is the result of

FIG. 120.—*Crystals of hippuric acid.* (Funke.)

FIG. 121.—*Lactate of lime, from chemically pure lactic acid and carbonate of lime, crystallized from a hot, watery solution.* (Funke.)

the transformation of glucose. As a curious chemical fact, it is interesting to note that the lactic acid contained in the lactates extracted from the muscular substance is not absolutely identical with the acid resulting from the transformation of the sugars. The former have been called sarcolactates, and they contain one equivalent of water less than the ordinary lactates. According to Robin, the compounds of lactic acid in the urine are in the form of sarcolactates.

Although the inosates have never been detected in the urine, Robin is of the opinion that traces of these salts are separated from the blood by the kidneys, from the fact that they exist normally in the blood and in the muscular tissue.

We have little or no information with regard to the relations of the inosates to excretion.

Creatine and Creatinine.—Creatine and creatinine are undoubtedly identical in their relations to the general process of disassimilation, for one is easily converted into the other, out of the body, by very simple chemical means; and there is every reason to suppose that, in the organism, they are the products of physiological waste of the same tissue or tissues. These principles have been found in the urine, blood, muscular tissue, and brain. Scherer has demonstrated the presence of creatine in the amniotic fluid. By certain chemical manipulations, both creatine and creatinine may be converted into urea; and the fact that these substances are now known to be constant constituents of the urine leaves no doubt that they are to be classed among the excrementitious principles. Chevreul, who first discovered creatine in the extract of muscular tissue, regarded it as one of the nutritive principles of meat; but the subsequent researches of Heintz, Liebig, and others, who found it in the urine, revealed its true character. Verdeil and Marcet have since found both creatine and creatinine in the blood; and these principles are now generally regarded as excrementitious matters, taken from the tissues by the blood, to be eliminated by the kidneys.

Creatine has a bitter taste, is quite soluble in cold water (one part in seventy-five), and is much more soluble in hot water, from which it separates in a crystalline form on cooling. It is but slightly soluble in alcohol and is insoluble in ether. A watery solution of creatine is neutral. It does not readily form combinations as a base; but it has lately been made to form crystalline compounds with some of the strong mineral acids, the nitric, hydrochloric, and sulphuric. When boiled for a long time with baryta, it is changed into urea and sarcosine; but the recent researches of Voit have pretty conclusively shown that this change does not take place in the living organism, and that probably none of the urea of the urine is produced in this way. When boiled with the strong acids, creatine loses four atoms of water and is converted into creatinine. This change takes place very readily in decomposing urine, which contains neither urea nor creatine but a large quantity of creatinine, when far advanced in putrefaction.

FIG. 122.—*Creatine, extracted from the muscular tissue, and crystallized from a hot, watery solution.* (Funke.)

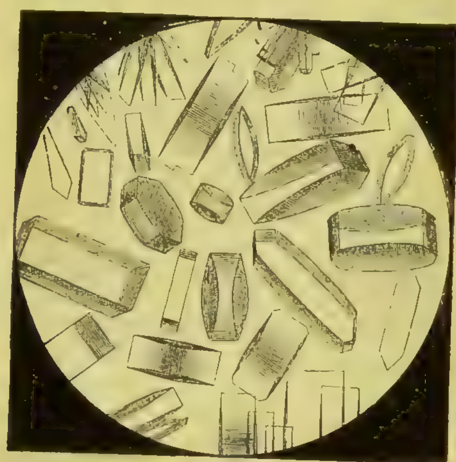


FIG. 123.—*Creatinine, formed from creatine by digestion with hydrochloric acid, and crystallized from a hot, watery solution.* (Funke.)

Creatinine is more soluble than creatine, and its watery solution has a strongly alkaline reaction. It is dissolved by eleven parts of cold water and is even more soluble in boiling water. It is slightly soluble in ether and is dissolved by one hundred parts of alcohol. This substance is regarded as one of the most powerful of the organic bases, readily forming crystalline combinations with a number of acids. According to Thudichum, who has very closely studied the physiological relations of these substances, creatine is the original excrementitious principle produced in the muscular substance, and creatinine is formed in the blood by a transformation of a portion of the creatine, somewhere between the muscles and the kidneys; "for, in the muscle, creatine has by far the preponderance over creatinine; in the urine, creatinine over creatine."

In the present state of our knowledge, there is very little to be said with regard to the physiological relations of creatine and creatinine, except that they are probably to be classed among the excrementitious principles resulting from the disassimilation of the muscular tissue. As they exist in considerable quantity in the muscular substance, it becomes a question whether, in the urine of carnivorous animals, they be not derived from the food; but they could have no such origin in the herbivora or in the urine of starving animals.

It has been assumed by many authors that, inasmuch as the muscular tissue of the heart is in almost constant action, it should contain more creatine than any other portion of the muscular system; but late observations on this point show that the reverse of this is the case. In comparing the proportion of creatine in the heart and in the muscles of the extremities, in oxen and in the human subject, the quantity has been found to be much less in the heart; still, the proportion of creatine has been found to be greater in tetanized muscles than in the muscular tissue after repose.

From the meagreness of our facts with regard to the physiological relations of creatine and creatinine, it is evident that there is much to be learned before we can understand the process of their formation in the healthy organism and the probable results of their retention or deficient elimination in disease. At present we can only say that these principles are probably produced in greatest part in the muscular tissue. The fact that creatine has lately been demonstrated in the brain would lead to the supposition that it is also one of the products of disassimilation of the nervous substance.

The average daily excretion of creatine and creatinine is estimated by Thudichum at about 11·5 grains. Of this he estimates that 4·5 grains consist of creatine, and 7 grains, of creatinine.

Oxalate of Lime.—This salt is not constantly present in the normal human urine, although it may exist in considerable quantity without indicating any pathological condition. It is exceedingly insoluble, and the appearance of its crystals, which are commonly in the form of small, regular octahedra, is quite characteristic. According to Robin, a trace may be retained in solution by the chlorides and the alkaline phosphates in the urine. This salt may find its way out of the system by the kidneys, after it has been taken with vegetable food or with certain medicinal substances. The ordinary rhubarb, or pie-plant, contains a large quantity of oxalate of lime, which, when this article is taken, will pass into the urine. It is probable, however, that a certain quantity of oxalate of lime may be formed in the organism. Pathologists now recognize a condition called oxaluria, characterized by the appearance of oxalate-of-lime crystals in the urinary sediments; and sometimes the quantity in the urine is so large, and its presence is so constant, that it forms vesical calculi of considerable size.

FIG. 124.—*Crystals of oxalate of lime, deposited from the normal human urine, on the addition, to the urine, of oxalate of ammonia.* (Funke.)

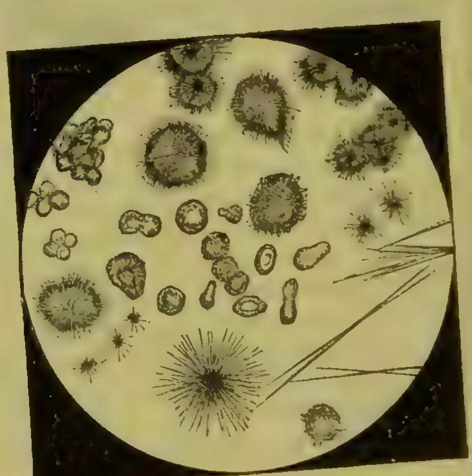


FIG. 125.—*Crystals of leucine.* (Funke.)

Inasmuch as pathological facts have shown pretty conclusively that oxalic acid may appear in the system without being introduced with the food, some physiologists have endeavored to show how it may originate from a change in certain other of the proximate principles from which it can be produced artificially out of the body. One of the substances from which oxalic acid can be thus formed is uric acid. It remains, however, to show that this can take place in the living organism. Woehler and Frerichs injected into the jugular vein of a dog a solution containing about twenty-three grains of urate of ammonia. In the urine, taken a short time after, there was no deposit of uric acid but there appeared numerous crystals of oxalate of lime. The same result followed in the human subject, on the administration of sixty-seven grains of urate of ammonia by the mouth. These questions have more of a pathological than a physiological interest; for the quantity of oxalate of lime in the normal urine is insignificant, and this salt does not seem to be connected with any of the well-known processes of disassimilation.

Xanthine, Hypoxanthine, Leucine, Tyrosine, and Taurine.—Traces of xanthine have been found in the normal human urine, but its proportion has not been estimated, and we are as yet but imperfectly acquainted with its physiological relations. Under patho-

FIG. 126.—*Crystals of tyrosine.* (Funke.)

FIG. 127.—*Crystals of taurine.* (Funke.)

logical conditions, it occasionally exists in sufficient quantity to form urinary calculi. It has been found in the liver, spleen, thymus, pancreas, muscles, and brain. It is insoluble in water but is soluble in both acid and alkaline fluids. Hypoxanthine has never been found in normal urine, although it exists in the muscles, liver, spleen, and thymus. Leucine exists in the pancreas, salivary glands, thyroid, thymus, suprarenal capsules, lymphatic glands, liver, lungs, kidneys, and in the gray substance of the brain. It has never been detected in the normal urine. The same remarks apply to tyrosine (although it is not so extensively distributed in the economy), to taurine and cystine. The last two, however, contain sulphur, and they may have peculiar physiological and pathological relations that we do not at present understand.

These various substances are mentioned, although some of them have not been demonstrated in the normal urine, for the reason that there is evidently much to be learned with regard to the various products of disassimilation as they are represented by the composition of the urine. While some of these may not be actual proximate principles, but substances produced by the processes employed for their extraction, some, which have thus far been discovered only under pathological conditions, may yet be found in health, and they represent, perhaps, important physiological acts.

Fatty Matters.—Fat and fatty acids are said to exist in the normal urine in certain quantity. Their proportion, however, is small, and the mere fact of their presence, only, is of physiological interest.

Inorganic Constituents of the Urine.

It is by the kidneys that the greatest quantity and variety of inorganic principles are discharged from the organism; and it is probable that even now we are not acquainted with the exact proportion and condition of all the principles of this class contained in the urine. In all the processes of nutrition, it is found that the inorganic constituents of the blood and tissues accompany the organic matters in their various transformations, although they are themselves unchanged. In fact, the condition of union of the inorganic with the organic principles is so intimate, that they cannot be completely separated without incineration. In view of these facts, it is evident that a certain part, at least, of the inorganic salts of the urine is derived from the tissues, of which, in combination with organic matters, they have formed a constituent part. As the kidneys frequently eliminate from the blood foreign matters taken into the system and are capable sometimes of throwing off an excess of the normal principles which may be introduced into the circulation, it can be readily understood how a large proportion of some of the inorganic matters of the urine may be derived from the food.

From the fact that the inorganic matters discharged in the urine are generally the same as those introduced with the food, and that they vary in proportion with the constitution of the food, it is difficult to ascertain how far their presence and quantity in the urine represent the processes of disassimilation. One thing, however, is certain: that the organic constituents of the food, the blood, the tissues, and the urine, are never without inorganic matter in considerable variety; and it is more than probable that the presence of these salts in a tolerably definite proportion influences the processes of absorption and secretion and has an important bearing upon nutrition; but we are as yet so imperfectly acquainted with the processes of nutrition of the tissues, that we cannot follow out all the relations of the inorganic matters, first to nutrition, and afterward to disassimilation.

Chlorides.—Almost all of the chlorine in the urine is in the form of chloride of sodium, the amount of chloride of potassium being insignificant and not of any special physiological importance. It is unnecessary, in this connection, to describe the well-known properties of common salt, and the methods for determining its presence and proportion in the urine are fully treated of in works upon physiological chemistry. All that we have to consider is its importance and significance as a urinary constituent.

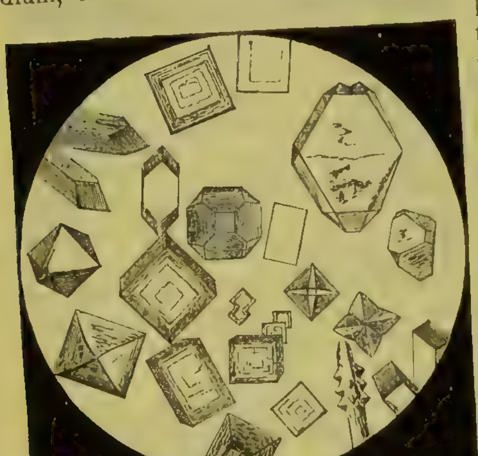


Fig. 128.—*Crystals of chloride of sodium.* (Funke.)

By reference to the table of the composition of the urine, it is seen that the proportion of chloride of sodium is subject to very great variations, the range being from three to eight parts per thousand. This at once suggests the idea that the quantity excreted is dependent to a considerable extent upon the amount taken in with the food; and, indeed, it has been shown by numerous observations that this is the fact. The proportion of chloride of sodium in the blood seems to be tolerably constant; and any excess that may be introduced is thrown off chiefly by the kidneys. It has been shown conclusively that deprivation of common salt in the food after a time is followed by serious disturbances in the general process of nutrition; and it is an acknowledged fact that this proximate principle is a constituent of every tissue of the body, except the enamel of the teeth. As the chlorides are deposited with the organic matter in all the acts of nutrition, they are found to be eliminated constantly with the products of disassimilation of the nitrogenized parts, and their absence from the food does not completely arrest their discharge in the urine. According to Robin, by suppressing salt in the food, its daily excretion may be reduced to from thirty to forty-five grains, the normal quantity being from one hundred and fifty to one hundred and sixty grains. This quantity is less than the amount contained in the ingesta, and under these circumstances there is a gradual diminution in the nutritive activity. "This fact demonstrates the necessity of adding chloride of sodium to the food." It is an interesting pathological fact that, in all acute febrile disorders, the proportion of chlorine in the urine rapidly diminishes and is frequently reduced to one hundredth of the normal amount. The quantity rapidly increases to the normal standard during convalescence. Most of the chlorides of the urine are in simple watery solution; but a certain proportion of the chloride of sodium exists in combination with urea.

The daily elimination of chloride of sodium is about one hundred and fifty-four grains (Robin). The great variations in its proportion in the urine, under different conditions of alimentation, etc., will explain the differences in the estimates given by various authorities.

Sulphates.—There is very little to be said regarding the sulphates, beyond the general statements we have made concerning the inorganic principles of the urine. The proportion of these salts in the urine is very much greater than in the blood, in which there exists only about 0·28 of a part per thousand. Inasmuch as the proportion in the urine is from three to seven parts per thousand, it seems probable that the kidneys eliminate these principles as fast as they find their way into the circulating fluid, either from the food or from the tissues. Like other principles derived in great part from the food, the normal variations in the proportion of sulphates in the urine are very great. It is unnecessary to consider in detail the variations in the amount of sulphates discharged in the urine, depending upon the ingestion of different salts or upon diet, for all the recorded observations have been followed by the same results, and they show that the ingestion of sulphates in quantity is followed by a corresponding increase in the proportion eliminated.

Thudichum estimates the daily excretion of sulphuric acid at from 23 to 38 grains. Assuming, with Robin, that the sulphates consist of about equal parts of sulphate of potassa and sulphate of soda, with traces of sulphate of lime, the quantity of salts would be from 22·5 to 37·5 grains of sulphate of potassa and an equal quantity of sulphate of soda.

Phosphates.—The urine contains phosphates in a variety of forms; but, inasmuch as it is not known that any one of the different combinations possesses peculiar relations to the process of disassimilation, as distinguished from the other phosphates, the phosphatic salts may be considered together.

The remarks which we have just made with regard to the chlorides and the sulphates are applicable, to a certain extent, to the phosphates. These salts exist constantly in the urine, and they are derived in part from the food and in part from the tissues. Like other inorganic matters, they are united with the nitrogenized elements of the organism, and, when these are changed into excrementitious principles and are separated from the blood by the kidneys, they pass with them and are discharged from the organism.

It becomes a question of importance, now, to consider how far the phosphates are derived from the tissues, and what proportion comes directly from the food. This point is peculiarly interesting, from the fact that phosphorus has been shown to exist in the nerve-tissue, and it has been inferred that the excretion of phosphates represents, to some extent, the physiological wear of the nervous system.

All observers agree that the quantity of phosphates in the urine is in direct relation to the proportion in the food, and that an excess of phosphates taken into the stomach is immediately thrown off by the kidneys. It is a familiar fact, indeed, that the phosphates are deficient and the carbonates predominate in the urine of the herbivora, while the reverse obtains in the carnivora, and that variations, in this respect, in the urine, may be produced by feeding animals with different kinds of food. Verdeil made some very interesting comparative analyses of the blood for the alkaline phosphates in the herbivora, the carnivora, and in man. He found the proportion very small in the ox, as compared with the dog, and intermediate in the human subject. The proportion of phosphates in the blood of the dog was greatly diminished by feeding with potato. Deprivation of food diminishes the quantity of phosphates in the urine, but a certain proportion is discharged, which is derived exclusively from the tissues. We have already noted the fact that the products of disassimilation of the nitrogenized principles are never discharged in health without being accompanied with certain inorganic salts, such as the chlorides, sulphates, and phosphates.

In connection with the fact that phosphorus exists (in precisely what condition it is not known) in the nervous matter, it has been stated that mental exertion is always attended with an increase in the elimination of phosphates; and this has been advanced to support the view that these salts are specially derived from disassimilation of the brain-substance. Experiments show that it is not alone the phosphates that are increased in quantity under these conditions, but urea, the chlorides, sulphates, and inorganic matters generally; and, in point of fact, any physiological conditions which increase the proportion of nitrogenized excrementitious principles increase as well the elimination of inorganic matters. It cannot be assumed, therefore, that the discharge of phosphates is specially connected with the activity of the brain. We learn nothing from pathology upon this point, for, although numerous observations have been made upon the excretion of phosphoric acid in disease—Vogel having made about one thousand different analyses in various affections—no definite results have been obtained. From these facts it is seen that there is no physiological reason why we should connect the elimination of the phosphates with the disassimilation of any particular tissue or organ, especially as these salts in some form are universally distributed in the organism.

Observations have been made upon the hourly variations in the discharge of phosphoric acid at different periods of the day; but these do not appear to bear any absolute relation to known physiological conditions, not even to the process of digestion.

Of the different phosphatic salts of the urine, the most important are those in which the acid is combined with soda. These exist in the form of the neutral and acid phosphates. The acid salt has one equivalent of the base and is supposed to be the source of the acidity of the urine at the moment of its emission. The so-called neutral salt is slightly alkaline and has two equivalents of the base. The proportion of the phosphates of soda in the urine is larger than that of any of the other phosphatic salts, but the daily amount excreted has not been estimated. The phosphate of magnesia is a constant constituent of the urine, as well as the acid and the basic phosphate of lime. The daily excretion of phosphate of magnesia amounts to from 7·7 to 11·8 grains, and that of the phosphates of lime, from 4·7 to 5·7 grains. According to Robin, there always exists in the urine a small quantity of the ammonio-magnesian phosphate, but it never, in health, exists in sufficient quantity to form a crystalline deposit. The daily excretion of the phosphates is, as we have seen, subject to great variations, but the average quantity of phosphoric acid excreted daily may be estimated at about fifty grains, or, more accurately, fifty-six grains.

The urine contains, in addition to the inorganic principles above described, a small quantity of silicic acid; but, as far as we know, this has no physiological importance.

Coloring Matter and Mucus.

The peculiar color of the urine is due to the presence of a nitrogenized principle, known to physiological chemists under a variety of names. We have mentioned it in the table as urrosacine. It is also called urochrome, urohæmatine, uroxanthine, and purpurine. We have no accurate account of its ultimate composition, and all that is known about its constituents is that it contains carbon, oxygen, hydrogen, and nitrogen, and probably iron. Although its exact ultimate composition is not absolutely settled, its constituents are supposed to be nearly the same as those of the coloring matter of the blood.

the proportion of oxygen being very much greater. These facts point to the probability of the formation of urrosacine from hæmaglobine.

The quantity of coloring matter in the normal urine is very small. It is subject to considerable variation in disease, and almost always it is fixed by deposits and calculi of uric acid or the urates, giving them their peculiar color. This principle first makes its appearance in the urine and is probably formed in the kidneys. So little is known of its physiological or pathological relations to the organism, that it does not seem necessary to follow out all of the chemical details of its behavior in the presence of different reagents.

The normal urine always contains a small quantity of mucus, with more or less epithelium from the urinary passages, and a few leucocytes. These form a faint cloud in the lower strata of healthy urine after a few hours' repose. The properties of the different kinds of mucus have already been considered. An important peculiarity, however, of the mucus contained in normal urine is that it does not seem to excite decomposition of the urea, and that the urine may remain for a long time in the bladder without undergoing any putrefactive change.

Gases of the Urine.

In the process of separation of the urine from the blood by the kidneys, a certain proportion of the gases in solution in the circulating fluid is also removed. For a long time, indeed, it has been known that the normal human urine contained different gases, but lately some very interesting observations on this subject have been made by M. Morin, in which the proportions of the free gases in solution have been accurately estimated. By using the method employed by Magnus in estimating the gases of the blood, Morin was able to extract about two and a half volumes of gas from a hundred parts of urine. By careful experiments, he ascertained that a certain quantity of gas remained in the urine and could not be extracted by his ordinary process. This amounted to about one-fifth of the whole volume of gas. Adding this to the quantity of gas extracted, he obtained the proportions to one litre of urine, in cubic centimetres, which are given in the table, viz.:

Oxygen	0·824
Nitrogen	9·589
Carbonic acid	19·620

These proportions represent the average of fifteen observations upon the urine secreted during the night.

The proportion of these gases was found by Morin to be subject to certain variations. For example, after the ingestion of a considerable quantity of water or any other liquid, the proportion of oxygen was considerably increased (from 0·824 to 1·024), and the carbonic acid was diminished more than one-half. The most interesting variations, however, were in connection with muscular exercise. After walking a long distance, the exercise being taken both before and after eating, the quantity of carbonic acid was found to be double that contained in the urine after repose. The proportion of oxygen was very slightly diminished, and the nitrogen was somewhat increased. The variations of these gases, however, were insignificant.

Morin explains the great increase in the proportion of carbonic acid, by the greater respiratory activity during exercise. It is well known, indeed, that muscular exercise largely increases the proportion of carbonic acid in the blood and the quantity eliminated by the lungs; and, as the carbonic acid of the urine is undoubtedly derived from the blood, we should expect that the same conditions would increase its proportion in this secretion.

It is not probable that the kidneys are very important as eliminators of carbonic acid from the system, but it is certain that the presence of this gas in the urine assists in the solution of some of the saline constituents of this fluid, notably the phosphates.

Variations in the Composition of the Urine.

The urine represents, in its varied constituents, not only a great part of the physiological disintegration of the organism, but it contains elements evidently derived from the food. Its constitution is varying with every different condition of nutrition, with exercise, bodily and mental, with sleep, age, sex, diet, respiratory activity, the quantity of cutaneous exhalation, and, indeed, with every condition that affects any part of the system. There is no fluid in the body that contains such a variety of principles, as a constant condition, but in which the proportion of these principles is so variable. It is for this reason that we have given in the table of the composition of the urine the ordinary limits of variation of its different constituents; and it has been found necessary, in treating of the individual excrementitious principles, to refer to some of the variations in their proportion in the urine. In treating more specially of the physiological variations of the urine, we shall only refer in general terms to conditions that produce wide and important changes in the proportion of its constituents; and, under the head of nutrition, we shall consider how far the absolute quantities of the urinary principles and other excrementitious substances represent the physiological waste which is always coincident with the repair of the parts.

Variations with Age and Sex.—There are decided differences in the composition of the urine at different periods of life and in the sexes. These undoubtedly depend in part upon the different conditions of nutrition and exercise, and in part upon differences in the food. Although the quantities of excrementitious matters present great variations, their relations to the organism are not materially modified, except, perhaps, at an early age; and the influence of sex and age operates merely as these conditions affect the diet and the general habits of life.

It is stated by most authors that the urine of the fœtus is highly albuminous and contains no urea; but examinations of the urine in the fœtus and newly born have been so few that we know very little regarding its constitution and normal variations. The researches of the authorities on this subject, quoted by Parkes, leave the question of the composition of the urine in the fœtus and during the first days of extra-uterine life still uncertain. In a specimen of urine taken from a still-born child delivered with forceps, examined by Drs. Elliot and Isaacs, the presence of urea was determined. Dr. Beale found urea in a specimen taken at the seventh month.

With our present imperfect knowledge of the composition of the urine at the earliest periods of existence, it is impossible to deduce any conclusions regarding the production of the excrementitious principles at this time; and it would be unprofitable to detail the unsatisfactory and conflicting examinations to be found in works devoted specially to the urine. Observations upon children between the ages of three and seven are more definite. At this period of life, the amount of urea excreted in proportion to the weight of the body is about double that in the adult. The amount of chlorine in children is about three times the quantity in the adult; and the proportionate amount of other solid matters is also greater. The amount of water excreted by the kidneys in children, in proportion to the weight of the body, is very much greater than in the adult, being more than double. From eight years of age to eighteen, the urinary excretion becomes gradually reduced to the adult standard. It has been observed that crystals of oxalate of lime are much more frequent in the urine of children between four and fourteen years of age than in the adult.

There are not many definite observations on record upon the composition of the urine in the later periods of life. It has been shown, however, that there is a decided diminution, at this time, in the excretion of urea, and that the absolute quantity of urine is somewhat smaller.

The absolute quantity of the urinary excretion in women is less than in men, and the same is true of the proportionate amount of these principles to the weight of the body; still, the differences in the proportionate excretion are not very marked, and the amount of all these principles being subject to modifications from the same causes as in men, the small deficiency, in the few direct observations upon record, may be in part, if not entirely, explained by the fact that women usually perform less mental and physical work than men, and that their digestive system is generally not so active.

Variations at Different Seasons and at Different Periods of the Day.—The changes in the quantity and composition of the urine which may be directly referred to the conditions of digestion, temperature, sleep, exercise, etc., have long been recognized by physiologists; but it is difficult, if not impossible, so to separate these influences, that the true modifying value of each can be fully appreciated. For example, there is nothing which produces such marked variations in the composition of the urine as the digestion of food. So marked, indeed, is its influence, that some writers of authority incline to the belief that the greatest part of what have been regarded as the most important excrementitious matters is derived from the food and not from physiological disintegration of the tissues. Under strictly physiological conditions, the modifying influence of digestion must always complicate observations upon the effects of exercise, sleep, season, period of the day, etc.; and the urine is continually varying in health, with the physiological modifications in the other processes and conditions of life. It will be sufficient for our purpose to note the most important of these variations and to endeavor to appreciate the conditions which combine to produce them, assigning to each one its proper value.

At different seasons of the year and in different climates, the urine presents certain variations in its quantity and composition. It seems necessary that a tolerably definite quantity of water should be discharged from the body at all times; and, when the temperature or the hygrometric condition of the atmosphere is favorable to the action of the skin, as in a warm, dry climate, the quantity of water in the urine is diminished, and its proportion of solid matters is correspondingly increased. On the other hand, the reverse obtains when the action of the skin is diminished from any cause. This fact is a matter of common remark as well as of scientific observation.

At different periods of the day, the urine presents constant and important variations. It is evident that the specific gravity must be constantly varying with the proportion of water and solid constituents. According to Dalton, the urine first discharged in the morning is dense and highly colored; that passed during the forenoon is pale and of a low specific gravity; and in the afternoon and evening it is again deeply colored, and its specific gravity is increased. The acidity is also subject to tolerably definite diurnal variations, which have already been noted.

Variations produced by Food.—An immense number of observations have been made upon the influence of ordinary food and upon diet restricted to particular articles. These facts have necessarily been considered more or less fully in connection with the origin of the urinary constituents; but it is important, in studying the influence of muscular exercise, mental effort, etc., to constantly bear in mind the variations occurring under the influence of the ingesta.

Water and liquids generally increase the proportion of water in the urine and diminish the specific gravity. This is so marked after the ingestion of large quantities of liquids, that the urine passed under these conditions is sometimes spoken of by physiologists as the urina potus. This must be borne in mind in clinical examinations of the urine. It is a curious fact, however, that, when an excess of water has been taken for purposes of experiment, the diet being carefully regulated, the absolute amount of solid matters excreted is considerably increased. This is particularly marked in the urea, but it is noticeable in the sulphates and phosphates, though not to any great extent in the chlorides. The results of experiments upon this point seem to show that water taken in excess increases the activity of disassimilation.

The ordinary meals invariably increase the solid constituents of the urine, the most constant and uniform increase being in the proportion of urea. This, however, depends to a great extent upon the kind of food taken. The increase is usually noted during the first hour after a meal, and it attains its maximum at the third or fourth hour. The inorganic matters are increased as well as the excrementitious principles proper. The urine passed after food has been called urina cibi, under the idea that it is to be distinguished from the urine supposed to be derived exclusively from disassimilation of the body, which is called the urina sanguinis.

It is an interesting and important question to determine the influence of different kinds of food upon the composition of the urine, particularly the comparative effects of a nitrogenized and a non-nitrogenized diet. Lehmann has made some very striking observations upon this point, and his results have been fully confirmed by many other physiologists of authority. Without discussing elaborately all of these observations, it is sufficient to state that the ingestion of an excess of nitrogenized principles always produced a great increase in the proportion of the nitrogenized constituents of the urine, particularly the urea. On a non-nitrogenized diet, the proportion of urea was found to be diminished more than one-half. The results of the experiments of Lehmann are so striking that we quote them in full:

"My experiments show that the amount of urea which is excreted is extremely dependent on the nature of the food which has been previously taken. On a purely animal diet, or on food very rich in nitrogen, there were often two-fifths more urea excreted than on a mixed diet; while, on a mixed diet, there was almost one-third more than on a purely vegetable diet; while, finally, on a non-nitrogenous diet, the amount of urea was less than half the quantity excreted during an ordinary mixed diet.

"In my experiments on the influence of various kinds of food on the animal organism, and especially on the urine, I arrived at the above results, which in mean numbers may be expressed as follows: On a well-regulated mixed diet I discharged, in twenty-four hours, 32·5 grammes of urea (I give the mean of fifteen observations); on a purely animal diet, 53·2 grammes (the mean of twelve observations); on a vegetable diet, 22·5 grammes (the mean of twelve observations); and on a non-nitrogenous diet, 15·4 grammes (the mean of three observations)."

With regard to the influence of food upon the inorganic constituents of the urine, it may be stated in general terms that the ingestion of mineral substances increases their proportion in the excretions. We have already alluded to this fact in treating of the different inorganic salts.

There are certain articles which, when taken into the system, the diet being regular, seem to retard the process of disassimilation; or, at least, they diminish, in a marked manner, the amount of matters excreted, particularly urea. Alcohol has a very decided influence of this kind. Its action may be modified by the presence of salts and other matters in the different alcoholic beverages, but, in nearly all direct experiments, alcohol, either taken under normal conditions of diet, when the diet is deficient, or when it is in excess, diminishes the excretion of urea. The same may be stated in general terms of tea and coffee.

Influence of Muscular Exercise.—There can be no doubt that muscular exercise, under ordinary conditions of diet, increases the proportion of many of the solid constituents of the urine, particularly the urea; but it must be remembered, in considering the effects of exercise upon the elimination of excrementitious matters, that the modifications in the urine produced by food are very considerable. We have purposely considered the influence of food before taking up other modifying conditions, so as to make apparent an important element of error in some recent observations which are at variance with the prevailing ideas on this subject. When, for example, it has been shown that restriction to a non-nitrogenous diet will immediately diminish the daily elimination of urea more than one-half, it is evident that the diet must always be fully considered in experiments upon the effects of exercise or of other modifying circumstances.

There is another important point, also, which is not always taken into consideration in comparative observations upon the absolute quantities of urea eliminated during exercise and repose; and that is the elimination of this principle by the cutaneous surface. We have already seen that urea is a constant constituent of the sweat. Speck, who found that exercise usually increased the elimination of excrementitious matters, noted the fact that urea was not increased in the urine when the sweat was very abundant.

A very elaborate analysis of the principal observations on this subject by Parkes shows the discrepancies in the experiments of different authors and points out several of the sources of error. The weight of experimental evidence formerly was decidedly in favor of an increase in the elimination of urea by exercise; and the observations opposed to this view involved inaccuracies which would explain, in part at least, the contradictory results obtained. Lately, however, new observations have been made, which are assumed by some to show an actual diminution by exercise in the quantity of urea excreted. Fick and Wislicenus, Frankland, and Haughton, have attempted to show that this is the fact, and these physiologists have come to the conclusion that muscular force involves chiefly the consumption of non-nitrogenous principles and the production of carbonic acid. While the experiments upon this subject have been so meagre, it would be unprofitable to enter into an elaborate discussion of their merits, particularly as they have not been directed specially to the influence of exercise upon the composition of the urine, but to the amount of muscular power developed by different kinds of food. This subject has not been reduced to such an absolute certainty that we are able to calculate mathematically the heat-units, the digestion-coefficients, and the amount of "work" produced by any given quantity of food; and such calculations cannot, as yet, take the place of actual experimental observations. What we want to know is the measurable influence of muscular exercise upon the proportion of certain of the constituents of the urine, under normal alimentation, every other modifying condition being taken into account. There can be no doubt that, under an ordinary mixed diet, the elimination of urea is increased by exercise. Fick and Wislicenus made their observations, extending over a period of between one and two days, under a diet of non-nitrogenized matter; and Prof. Haughton compared his observations, made in July, with an average of experiments made at different seasons, taking no account of the action of the skin. It may be true that, with a purely non-nitrogeneous diet, exercise fails to increase the quantity of urea eliminated by the kidneys, as appears from the observations of Fick and Wislicenus; but farther experiments are necessary to settle even this point, and the recent observations by Parkes show that this is not always the case.

With regard to the influence of muscular exercise upon the other constituents of the urine, experiments are somewhat contradictory. Sometimes the water is lessened and sometimes it is increased; this difference probably depending upon the activity of the cutaneous exhalation. Sometimes the uric acid is increased and sometimes it is diminished. The sulphates, phosphates, and chlorides, are generally increased.

The general result of experimental observations on the effects of exercise upon the urine may be summed up in the proposition that this condition increases the activity of the nutritive processes, and produces a corresponding activity in the function of disassimilation, as indicated by the amount of excrementitious matters separated by the kidneys.

We have had an opportunity of settling definitely the vexed question of the influence of muscular exercise upon the elimination of nitrogen.[1] In 1871, we made an exceedingly

[1] FLINT, JR., *On the Physiological Effects of Severe and Protracted Muscular Exercise, with special Reference to its Influence upon the Excretion of Nitrogen.—New York Medical Journal*, 1871, vol. xiii., p. 609, *et seq.*

elaborate series of observations upon Mr. Weston, the pedestrian. Of these we can only give here a brief summary. Mr. Weston walked for five consecutive days as follows: First day, 92 miles; second day, 80 miles; third day, 57 miles; fourth day, 48 miles; fifth day, 40½ miles. The nitrogen of the food was compared with the nitrogen excreted for three periods; viz., five days before the walk, five days walking, and five days after the walk. A trusty assistant was with Mr. Weston day and night for the fifteen days; the food was weighed and analyzed; the excreta were collected; and other observations were made during the entire period. The analyses were made independently, under the direction of Prof. R. O. Doremus, who had no idea of the results until we had classified and tabulated them. The conclusions were most decided, and, as far as possible, all the physiological conditions were fulfilled. As regards the proportion of nitrogen eliminated to the nitrogen of the food, the general results were as follows:

For the five days before the walk, with an average exercise of about eight miles daily, the nitrogen eliminated was 95·53 parts for 100 parts of nitrogen ingested. For the five days of the walk, for every hundred parts of nitrogen ingested, there were discharged 174·81 parts. For the five days after the walk, when there was hardly any exercise, for every hundred parts of nitrogen ingested, there were discharged 91·93 parts. During the walk, the nitrogen excreted was in direct ratio to the amount of exercise; and, what was still more striking, the excess of nitrogen eliminated over the nitrogen of food almost exactly corresponded with a calculation of the nitrogen of the muscular tissue wasted, as estimated from the loss of weight of the body. Full details of the method of investigation, the processes employed, etc., are given in our original paper.

Influence of Mental Exertion.—Although the influence of mental exertion upon the composition of the urine has not been very closely studied, the results of the investigations which have been made upon this subject are, in many regards, quite satisfactory. It is a matter of common remark that the secretion of urine is often modified to a considerable extent through the nervous system. Fear, anger, and various violent emotions, sometimes produce a sudden and copious secretion of urine containing a large amount of water, and this phenomenon is often observed in cases of hysteria. Intense mental exertion will occasionally produce the same result. We have often observed a frequent desire to urinate during a few hours of intense and unremitting mental labor; and, on one occasion, being struck with the amount of urine voided, it was found, on examination, to present scarcely any acidity, and a specific gravity of about 1002. The interesting point in this connection, however, is to observe the influence of mental labor upon the elimination of solid matters, as contrasted with the amount of excretion during complete repose, the conditions of alimentation in the two instances being identical.

In a very interesting work upon the influence of cerebral activity upon the composition of the urine, Byasson found that by mental exertion the quantity of urine was increased; the amount of urea was also increased; the phosphoric acid was increased about one-third; the sulphuric acid was more than doubled; and the chlorine was nearly doubled.

These facts have an important bearing upon our knowledge of the effects of mental exertion upon the process of disassimilation of the nervous tissue. They show that nearly all of the solid principles contained in the urine are increased in quantity by prolonged intellectual exertion, but they fail to point to any one excrementitious principle, either organic or inorganic, which is specially connected with the physiological wear of the brain. It has been assumed that elimination of the phosphates, increased out of proportion to the increase of the other solid matters of the urine, is one of the constant effects of intellectual effort; but this view is not sustained by direct physiological experiments or by facts in pathology. We have already discussed this question somewhat elaborately, under the head of the phosphates of the urine.

CHAPTER XIII.

FUNCTIONS OF THE LIVER.

Physiological anatomy of the liver—Distribution of the portal vein, the hepatic artery, and the hepatic duct—Origin and course of the hepatic veins—Structure of a lobule of the liver—Arrangement of the bile-ducts in the lobules—Anatomy of the excretory biliary passages—Nerves and lymphatics of the liver—Mechanism of the secretion and discharge of bile—Quantity of bile—Variations in the flow of the bile—Discharge of bile from the gall-bladder—General properties of the bile—Composition of the bile—Origin of the biliary salts—Cholesterine—Biliverdine—Tests for bile—Excretory function of the liver—Origin of cholesterine—Experiments showing the passage of cholesterine into the blood as it circulates through the brain—Elimination of cholesterine by the liver—Cholesteræmia—Production of sugar in the liver—Evidences of a glycogenic function in the liver—Does the liver contain sugar during life?—Mechanism of the production of sugar by the liver—Glycogenic matter—Variations in the glycogenic function—Production of sugar in fœtal life—Influence of digestion and of different kinds of food upon glycogenesis—Influence of the nervous system, etc., upon glycogenesis—Artificial diabetes—Destination of sugar—Alleged production of fat by the liver—Changes in the albuminoid and the corpuscular elements of the blood in their passage through the liver.

Physiological Anatomy of the Liver.

The liver, by far the largest gland in the body, is now known to have several entirely distinct functions; and one of the most important of these has already been fully considered, in connection with digestion. It is true that we know very little with regard to the exact office of the bile in digestion, but that this function is essential to life, there can be no doubt. We have, however, more positive information with regard to the excrementitious function of the liver and the changes which the blood undergoes in passing through its substance; and the study of these functions is closely connected with the anatomy of the liver and the chemical constitution of the bile.

It is unnecessary, in this connection, to dwell upon the ordinary descriptive anatomy of the liver. It is sufficient to state that it is situated just below the diaphragm, in the right hypochondriac region, and is the largest gland in the body, weighing, when moderately filled with blood, about four and a half pounds. Its weight is somewhat variable, but it is stated by Sappey that, in a person of ordinary adipose development, its proportion to the weight of the body is about as one to thirty-two. In early life, the liver is relatively larger, its proportion to the weight of the body, in the new-born child, being as one to eighteen or twenty.

The liver is covered externally by peritoneum, folds or duplicatures of this membrane being formed as it passes from the surface of the liver to the adjacent parts. These constitute four of the so-called ligaments that hold the liver in place. The proper coat of the liver is a very thin but dense and resisting fibrous membrane, adherent to the substance of the organ, but detached without much difficulty, and very closely united to the peritoneum. This membrane is of variable thickness at different parts of the liver, being especially thin in the groove for the vena cava. At the transverse fissure, it surrounds the duct, blood-vessels, and nerves, and it penetrates the substance of the organ in the form of a vagina, or sheath, surrounding the vessels and branching with them. This membrane, as it ramifies in the substance of the liver, is called the capsule of Glisson. It will be more fully described in connection with the arrangement of the hepatic vessels.

The substance of the liver is made up of innumerable lobules, of an irregularly ovoid or rounded form, and about $\frac{1}{20}$ of an inch in diameter. The space which separates these lobules is about one-quarter of the diameter of the lobule and is occupied with the blood-vessels, nerves, and ramifications of the hepatic duct, all enclosed in the fibrous sheath. In a few animals, as, for example, the pig and the polar bear, the division of the hepatic substance can be readily made out with the naked eye; but, in man and in most of the mammalia, the lobules are not so distinct, although their arrangement is essentially the same. Although the lobules are intimately connected with each other from the fact that branches going to a number of different lobules are given off from the same interlobular vessels, they are sufficiently distinct to represent, each one, the general anatomy of the secreting substance of the liver; but, before we study the minute structure of the lobules, it will be convenient to follow out the course of the vessels and the duct, after they have penetrated at the transverse fissure. In this description we shall follow, in the main, the observations of Kiernan, who has given, probably, the most accurate account of the vascular arrangement in the liver.

At the transverse fissure, the portal vein, collecting the blood from the abdominal organs, and the hepatic artery, a branch of the cœliac axis, penetrate the substance of the liver, with the hepatic duct, nerves, and lymphatics, all enveloped in the fibrous vagina, or sheath, known as the capsule of Glisson. The portal vein is by far the larger of the two blood-vessels, and its caliber may be roughly estimated at from eight to ten times that of the artery.

The vagina, or capsule of Glisson, is composed of fibrous tissue, in the form of a dense membrane, closely adherent to the adjacent structure of the liver, and enveloping the vessels and nerves, to which it is attached by a loose areolar tissue. The attachment of the blood-vessels to the sheath is so loose, that the branches of the portal vein are collapsed when not filled with blood; thus presenting a striking contrast to the hepatic veins, which are closely adherent to the substance of the liver and remain open when they are cut across. This sheath is prolonged over the vessels as they branch and it follows them in their subdivisions. It varies considerably in thickness in different animals. In man and in the mammalia generally, it is rather thin, becoming more and more delicate as the vessels subdivide, and it is entirely lost before the vessels are distributed in the interlobular spaces.

The vessels distributed in and coming from the liver are the following:

1. The portal vein, the hepatic artery, and the hepatic duct, passing in at the transverse fissure, to be distributed in the lobules. The blood-vessels are continuous in the lobules with the radicles of the hepatic veins. The duct is to be followed to its branches of origin in the lobules.

2. The hepatic veins; vessels that originate in the lobules, and collect the blood distributed in their substance by branches of the portal vein and of the hepatic artery.

Branches of the Portal Vein, the Hepatic Artery, and the Hepatic Duct.—These vessels follow out the branches of the capsule of Glisson, become smaller and smaller, and they finally pass directly between the lobules. In their course, however, they send off lateral branches to the sheath; and those who follow exactly the description of Kiernan call this the vaginal plexus. The arrangement of the vessels in the sheath is not in the form of a true, anastomosing plexus, although branches pass from this so-called vaginal plexus between the lobules. These vessels do not anastomose or communicate with each other in the sheath.

The portal vein does not present any important peculiarity in its course from the transverse fissure to the interlobular spaces. It subdivides, enclosed in its sheath, until its small branches go directly between the lobules, and, in its course, it sends branches to the sheath (vaginal vessels), which afterward go between the lobules. The distribution of the hepatic artery, however, is not so simple. This vessel has three sets of branches. As soon as it enters the sheath with the other vessels, it sends off minute branches (vasa vasorum), to the walls of the portal vein, to the larger branches of the artery itself, to the walls of the hepatic veins, and a very rich net-work of branches to the hepatic duct. When the hepatic artery is completely injected, the walls of the hepatic duct are seen almost covered with vessels. In its course, the hepatic artery also sends branches to the capsule of Glisson (capsular branches), which join with the branches of the portal vein, to form the so-called vaginal plexus. From these vessels, a few arterial branches are given off which pass between the lobules. The hepatic artery cannot be followed beyond the interlobular spaces. The terminal branches of the hepatic artery are not directly connected with the radicles of the hepatic veins, but they empty into small branches of the portal vein within the capsule of Glisson.

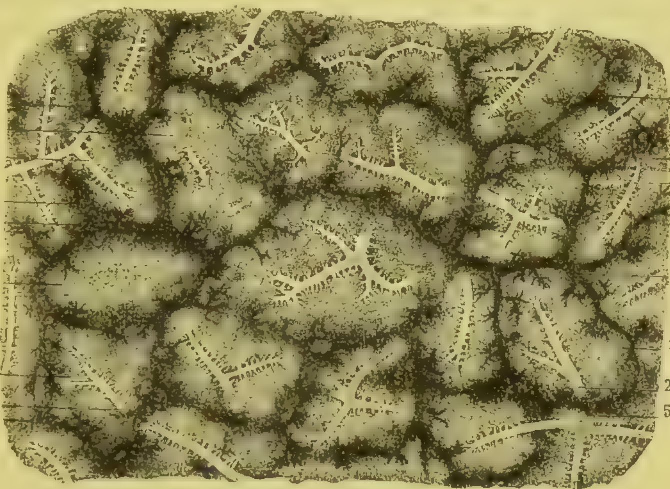


FIG. 129.—*Lobules of the liver, interlobular vessels, and intralobular veins.* (Sappey.)
1, 1, 1, 1, 3, 4, lobules; 2, 2, 2, 2, intralobular veins, injected with white; 5, 5, 5, 5, 5, interlobular vessels, filled with a dark injection.

The hepatic duct follows the general course of the portal vein; but its structure and relations are so important and intricate that they will be described separately.

Interlobular Vessels.—Branches of the portal vein, coming from the terminal ramifications as the vessel branches within the capsule and from the branches in the walls of the capsule, are distributed between the lobules, constituting the greatest part of the so-called interlobular plexus. These are situated between the lobules and surround them; each vessel, however, giving off branches to two or three lobules, and never to one alone. They do not anastomose, and consequently they are not in the form of a true plexus. The diameter of these interlobular vessels varies from $\frac{1}{1440}$ to $\frac{1}{720}$ of an inch. In this distribution, the blood-vessels are followed by branches of the duct, which are much less numerous and smaller, measuring only $\frac{1}{2500}$ of an inch; and some, even, have been measured that are not more than $\frac{1}{3000}$ of an inch in diameter.

Lobular Vessels.—In the interlobular plexus, the ramifications of the hepatic artery are lost, and this can no longer be traced as a distinct vessel. One of the peculiarities of its arrangement, as we have seen, is that the artery does not empty into the radicles of the efferent vein but joins the portal vessels as they are about to be distributed in a true capillary plexus in the substance of the lobules. In the lobules themselves, consequently, we have only to study the arrangement of the portal plexus, with the mode of origin of the hepatic veins and the relations of the hepatic duct.

The arrangement of the lobular plexus of blood-vessels is very simple. From the interlobular veins, a number of branches (eight to ten) are given off and penetrate the lobule. As the interlobular vessels are situated between different lobules, each one sends branches into two and sometimes three of these lobules; so that, as far as vascular supply is concerned, these divisions of the liver are never absolutely distinct.

After passing from the interlobular plexus into the lobules, the vessels immediately break up into a close net-work of capillaries, from $\frac{1}{3000}$ to $\frac{1}{2200}$ of an inch in diameter, which occupy the lobules with a true plexus. These vessels are very numerous; and, when they are fully distended by artificial injection, their diameter is greater than that of the intervascular spaces. It must be remembered, however, that, in the study of the liver by minute injections, as in other parts, the vessels probably are distended so that they occupy more space than they ever do under the physiological conditions of the circulation. The blood, having been distributed in the lobules by this lobular plexus, is collected by venous radicles of considerable size into a single central vessel situated in the long axis of the lobule, called the intralobular vein. A single lobule, surrounded with an interlobular vessel, showing the lobular capillary plexus, and the central vein (the intralobular vein) cut across, is represented in Fig. 130.

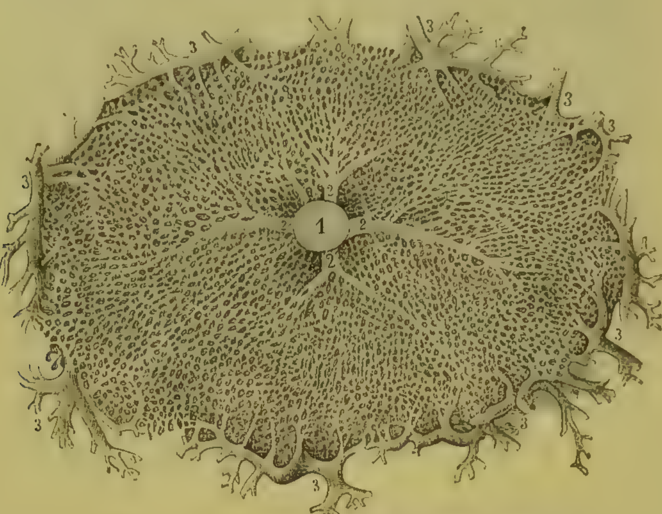


Fig. 130.—*Transverse section of a single hepatic lobule.* (Sappey.)
1, intralobular vein, cut across; 2, 2, 2, 2, afferent branches of the intralobular vein; 3, 3, 3, 3, 3, 3, 3, 3, 3, interlobular branches of the portal vein, with its capillary branches, forming the lobular plexus, extending to the radicles of the intralobular vein.

With regard to the mode of origin of the hepatic duct in the substance of the lobule, recent researches have shown that it begins by a very fine, anastomosing plexus of vessels, with amorphous walls, situated between the liver-cells; but there are many different opinions on this subject, and we shall defer its full consideration until we take up the anatomy of the secreting structures in the lobules.

Origin and Course of the Hepatic Veins.—The blood distributed in the lobular capillary plexus furnishes the materials for the formation of bile and undergoes those changes produced by the action of the liver as a ductless gland; in other words, it is in and around this plexus that all the physiological functions of the liver are performed. It is then only necessary that the blood should be carried from the liver to go to the right side of the heart; and the arrangement of the hepatic veins is accordingly very simple.

Intralobular Veins.—The innumerable capillaries of the lobules converge into three or four venous radicles (represented in Fig. 130), which empty into a central vessel, from $\frac{1}{1000}$ to $\frac{1}{400}$ of an inch in diameter. This is the intralobular vein. If a liver be carefully injected from the hepatic veins, and if sections be made in various directions, it will be seen that the intralobular veins follow the long axis of the lobules, receiving vessels in their course, until they empty into a larger vessel, situated at what may be termed the base of the lobules. These vessels have been called, by Kiernan, the sublobular veins. They collect the blood in the manner just described from all parts of the liver, unite with others, becoming larger and larger, until finally they form the three hepatic veins, which discharge the blood from the liver into the vena cava ascendens.

The hepatic veins differ somewhat in their structure from other portions of the venous system. Their walls are thinner than those of the portal veins, they are not enclosed in a sheath, and they are very closely adherent to the hepatic tissue. It is this provision which makes the force of aspiration from the thorax so efficient in the circulation in the liver. Here, indeed, a force added to the action of the heart is specially necessary; for the blood is passing into the liver through a second capillary plexus, having already been distributed in the capillaries of the alimentary canal and other abdominal organs, before it is received into the portal vein. It has also been noted that the hepatic veins possess a well-marked muscular tunic, very thin in man, but well-developed in the pig, the ox, and the horse, and composed of unstriped muscular fibres interlacing with each other in every direction.

In addition to the blood-vessels just described, the liver receives venous blood from vessels which have been called accessory portal veins, coming from the gastro-hepatic omentum, the surface of the gall-bladder, the diaphragm, and from the anterior abdominal walls. These vessels penetrate at different portions of the surface of the liver, and they may serve as derivatives, when the circulation through the portal vein is obstructed.

Structure of a Lobule of the Liver.—Each hepatic lobule, bounded and more or less distinctly separated from the others by the interlobular vessels, contains blood-vessels, radicles of the hepatic ducts, and the so-called hepatic cells. The arrangement of the blood-vessels has just been described; but, in all preparations made by artificial injection, the space occupied by the blood-vessels is exaggerated by excessive distention, and the difficulties in the study of the relations of the ducts and the liver-cells are thereby much increased. As the important problem in the minute anatomy of the lobules has been the relations of the cells to the radicles of the bile-ducts, we shall first take up the structure of the cells.

Hepatic Cells.—If a scraping from the cut surface of a fresh liver be examined with a moderately high magnifying power, the field of view will be found filled with numerous rounded, ovoid, or irregularly polygonal cells, measuring from $\frac{1}{1500}$ to $\frac{1}{1000}$ of an inch in diameter. In their natural condition, they are more frequently ovoid than polygonal; and, when they have the latter form, the corners are always rounded. These cells present one and sometimes two nuclei, sometimes with and sometimes without nucleoli. The presence of numerous small pigmentary granules gives to the cells a peculiar and characteristic appearance; and, in addition, nearly all of them contain a few granules or small globules of fat. Sometimes the fatty and pigmentary matter is so abundant as to obscure the nuclei. The addition of acetic acid renders the cells pale and the nuclei more distinct. By appropriate reagents, animal starch (probably glycogenic matter) has been demonstrated in the substance of the cells.

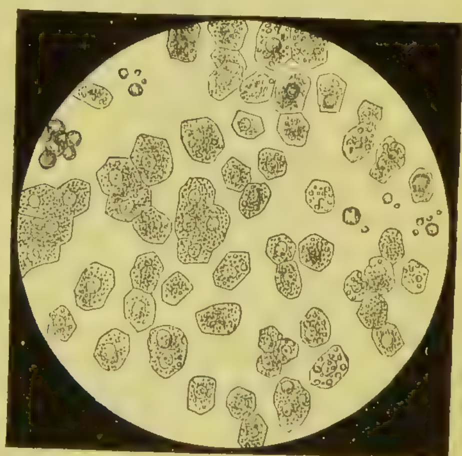


FIG. 131.—*Liver-cells, from a human, fatty liver.* (Funke.)

Arrangement of the Bile-ducts in the Lobules.—In describing the plexus of origin of the biliary ducts, we shall not discuss the views of Kiernan, Leidy, Beale, and others, as recent researches have conclusively shown that these were entirely erroneous. Late researches have shown that the following is probably the true relation of the ultimate ramifications of the bile-ducts in the lobules to the hepatic cells:

In the substance of the lobules, is an exceedingly fine and regular net-work of vessels, of uniform size, about $\frac{1}{10000}$ of an inch in diameter, which surround the liver-cells, each cell lying in a space bounded by inosculating branches of these canals. This plexus is entirely independent of the blood-vessels, and it seems to enclose in its meshes each individual cell, extending from the periphery of the lobule (where it is in communication with the interlobular bile-ducts) to the intralobular vein in the centre. The vessels probably have excessively thin, homogeneous walls—although the existence of their membrane has not been positively demonstrated—and are without any epithelial lining, being much smaller, indeed, than any epithelial cells with which we are acquainted. This arrangement, as far as is known, has no analogue in any other secreting organ.

FIG. 132.—*Portion of a transverse section of an hepatic lobule of the rabbit; magnified 400 diameters.* (Kölliker.)
b, b, b, capillary blood-vessels; *g, g, g,* capillary bile-ducts; *l, l, l,* liver-cells.

Although it is within a few years only that the reticulated bile-ducts of the lobules have attracted much attention, they were discovered in the substance of the lobules, near the periphery, by Gerlach, in 1848. It is evident, from an examination of his figures and description, that he succeeded in filling with injection that portion of the lobular net-work near the borders of the lobules, and he demonstrated the continuity of their vessels with the interlobular ducts; but he did not recognize the vessels nearer the centre of the lobule. It is now demonstrated, beyond a doubt, that there are either canals or interspaces between the liver-cells in the lobules, and that these open into the interlobular hepatic ducts. It is still a question of discussion, however, whether these passages be simple spaces between the cells or true vessels lined by a membrane; but this point has no great physiological importance, and we can readily imagine that it would be exceedingly difficult to demonstrate a membrane forming the wall of a tube, the whole measuring but $\frac{1}{10000}$ of an inch.

A peculiarly favorable opportunity for observing the bile-ducts in the lobules was presented in the livers of animals that died of the so-called "Texas cattle-disease." This was taken advantage of by the late Dr. R. C. Stiles, who was able to verify, in the most satisfactory manner, the facts which have lately been established by the German anatomists. In these livers, the finest bile-ducts were found filled with bright yellow bile, and their relations to the liver-cells were exceedingly distinct. In the examination of these specimens, the presence of what appeared to be detached fragments of these little canals is an argument in favor of the view that they are lined by a membrane of excessive tenuity. These interesting anatomical points were demonstrated by Dr. Stiles before the New York Academy of Medicine, and we have since been able to verify them in every particular.

Anatomy of the Excretory Biliary Passages.—There can be scarcely any doubt of the connection between the intercellular biliary plexus in the substance of the lobules and the interlobular ducts. We shall see, farther on, that the ducts, in their course from the lobules to the intestine, are provided with numerous small, racemose glands, which probably secrete a mucus that is mixed with the bile; but, in all probability, the peculiar elements of the bile are formed in the lobules, and the canals situated between the lobules and leading from them to the larger ducts are merely excretory.

Between the lobules, the ducts are very small, the smallest measuring about $\frac{1}{3000}$ of an inch in diameter. They are composed of a delicate membrane, lined with small, flattened epithelium. The ducts larger than $\frac{1}{1200}$ of an inch have a fibrous coat, formed of inelastic with a few elastic elements, and, in the larger ducts, there are, in addition, a few non-striated muscular fibres. The epithelium lining these ducts is of the columnar variety, the cells gradually undergoing a transition from the pavement-form as the ducts increase in size. In the largest ducts, there is a distinct mucous membrane, with mucous glands.

Throughout the whole extent of the biliary passages, from the interlobular canals to the ductus choledochus, are little utricular or racemose glands, varying in size in different portions of the liver, called by Robin, the biliary acini. These are situated, at short intervals, by the sides of the canals. The glands connected with the smallest ducts are simple follicles, from $\frac{1}{800}$ to $\frac{1}{400}$ of an inch long. The larger glands are formed of groups of these follicles, and they measure from $\frac{1}{250}$ to $\frac{1}{100}$ of an inch in diameter. The glands are only found connected with the ducts ramifying in the substance of the liver, and they do not exist in the hepatic, cystic, and common ducts. They are composed of a homogeneous membrane, lined with small, pale cells of pavement-epithelium. If the ducts in the substance of the liver be isolated, they are found covered with these little groups of follicles and have the appearance of an ordinary racemose gland, except that the acini are relatively small and scattered. This appearance is represented in Fig. 133.

FIG. 133.—*Anastomoses, and racemose glands attached to the biliary ducts of the pig; magnified* 18 *diameters.* (Sappey.)

1, 1, branch of an hepatic duct, with the surface almost entirely covered with racemose glands opening into its cavity; 2, branch in which the glands are smaller and less numerous; 3, 3, 3, branches of the duct with still simpler glands; 4, 4, 4, 4, biliary ducts with simple follicles attached; 5, 5, 5, 5, the same, with fewer follicles; 6, 6, 6, 6, 6, anastomoses in arches; 7, 7, 7, angular anastomoses; 8, 8, 8, 8, anastomoses by transverse branches.

The excretory biliary ducts, from the interlobular vessels to the point of emergence of the hepatic duct, present numerous anastomoses with each other in their course.

Vasa Aberrantia.—In the livers of old persons, and occasionally in the adult, certain vessels are found ramifying on the surface of the liver, but always opening into the biliary ducts, which have been called vasa aberrantia. These are never found in the fœtus or in children. They are, undoubtedly, appendages of the excretory system of the liver, and are analogous in their structure to the ducts, but are apparently hypertrophied, with thickened, fibrous walls, and present, in their course, irregular constrictions, not found in the normal ducts. The racemose glands attached to them are always very much atrophied. Sappey is of the opinion that these are ducts leading to lobules on the surface of the liver, which have become atrophied.

Gall-bladder, Hepatic, Cystic, and Common Ducts.—The hepatic duct is formed by the union of two ducts, one from the right and the other from the left lobe of the liver. It is about an inch and a half in length and joins at an acute angle with the cystic duct, to form the ductus communis choledochus. The common duct is about three inches in length, of the diameter of a goose-quill, and it opens into the descending portion of the duodenum. It passes obliquely through the coats of the intestine and opens into its cavity, in connection with the principal pancreatic duct. The cystic duct is about an inch in length and is the smallest of the three canals.

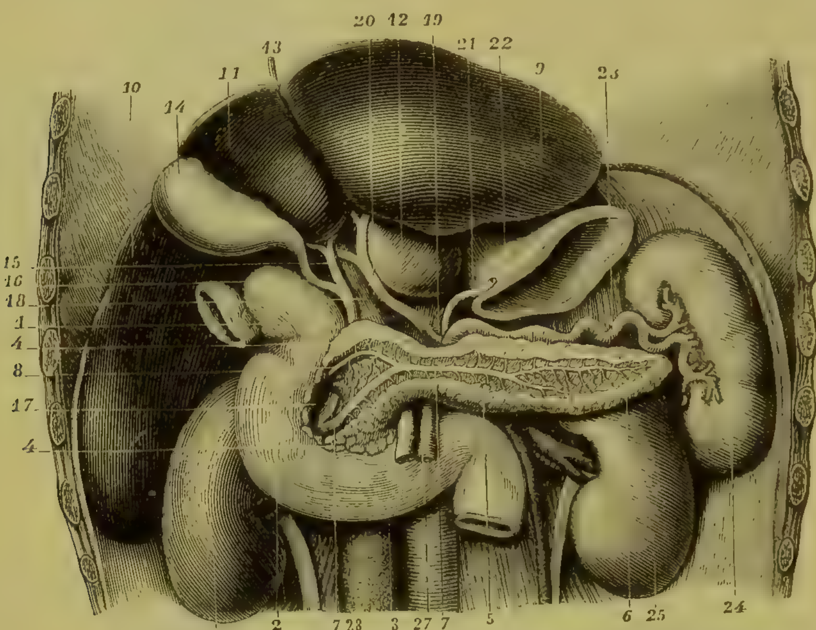


FIG. 134.—*Gall-bladder, hepatic, cystic, and common ducts.* (Sappey.)
1, 2, 3, duodenum; 4, 4, 5, 6, 7, 7, 8, pancreas and pancreatic ducts; 9, 10, 11, 12, 13, liver; 14, *gall-bladder;* 15, *hepatic duct;* 16, *cystic duct;* 17, *common duct;* 18, portal vein; 19, branch from the cœliac axis; 20, hepatic artery; 21, coronary artery of the stomach; 22, cardiac portion of the stomach; 23, splenic artery; 24, spleen; 25, left kidney; 26, right kidney; 27, superior mesenteric artery and vein; 28, inferior vena cava.

The structure of these ducts is essentially the same. They have a proper coat, formed of white fibrous tissue, a few elastic fibres, and a few non-striated muscular fibres. The muscular tissue is not sufficiently distinct to form a separate coat. The mucous membrane is always found tinged yellow with the bile, even in living animals. It is marked by numerous minute excavations and is covered with cells of columnar epithelium. This membrane contains numerous mucous glands.

The gall-bladder is an ovoid or pear-shaped sac, about four inches in length, one inch in breadth at its widest portion, and capable of holding from an ounce to an ounce and a half of fluid. Its fundus is covered entirely with peritoneum, but this membrane passes only over the lower surface of its body.

The proper coat of the gall-bladder is composed of white fibrous tissue with a few elastic fibres. In some of the lower animals there is a distinct muscular coat, but a few scattered fibres only are found in the human subject. The mucous coat is of a yellowish color and marked with numerous very small, interlacing folds, which are exceedingly vascular. Like the membrane of the ducts, the mucous lining of the gall-bladder is covered with columnar epithelium. In the gall-bladder, are found numerous small racemose glands, formed of from four to eight follicles lodged in the submucous structure. These are essentially the same as the glands opening into the ducts in the substance of the liver, and they secrete a mucus which is mixed with the bile.

Nerves and Lymphatics of the Liver.—The nerves of the liver are derived from the pneumogastric, the phrenic, and the solar plexus of the sympathetic. The branches of the left pneumogastric penetrate with the portal vein, while the branches from the right pneumogastric, the phrenic, and the sympathetic surround the hepatic artery and the hepatic duct. All of these nerves penetrate at the transverse fissure and follow the blood-vessels in their distribution. They have not been traced farther than the terminal ramifications of the capsule of Glisson, and their exact mode of termination is unknown.

The lymphatics of the liver are very numerous. They are divided into two layers: the superficial layer, situated just beneath the serous membrane; and the deep layer, formed of a plexus surrounding the lobules and situated outside of the blood-vessels. The superficial lymphatics from the under surface of the liver, and that portion of the deep lymphatics which follows the hepatic veins out of the liver, pass through the diaphragm and are connected with the thoracic glands. Some of the lymphatics from the superior or convex surface join the deep vessels that emerge at the transverse fissure and pass into glands below the diaphragm, while others pass into the thoracic cavity.

Mechanism of the Secretion and Discharge of Bile.—The liver has no analogue in the glandular system, either in its anatomy or in its physiology. There is no gland in the economy which we know to have two distinct functions, such as the secretion of bile and the production of certain elements destined to be taken up by the current of blood as it passes through. In other words, there is no organ in the body which has at the same time the functions of an ordinary secreting gland and a ductless gland. If we regard the liver-cells as the anatomical elements which produce the bile, it is evident that their number is very much out of proportion to the amount of bile secreted; and the liver itself is an organ of much greater size than it seems to us would be required for the mere secretion of bile. We explain this disproportionate size by the fact that the liver has other functions, which are those of a ductless gland.

There is no gland in which the arrangement of secreting tubes is the same as in the liver. It is hardly possible that the intercellular plexus of fine tubes in the lobules should be any thing but the plexus of origin, or the secreting portion of the hepatic duct. These are certainly not blood-vessels, and the only vessels that could have the appearance we have described, except the bile-ducts, are the lymphatics; but the communication between these vessels and the excretory bile-ducts, and the fact that they have been seen distended with bile in icteric livers, are pretty conclusive evidence of their nature. This arrangement, then, must be regarded as peculiar to the liver, as the arrangement of a capillary plexus surrounded with cells and enveloped in a dilated extremity of a secreting tube is peculiar to the kidney and is found in no other glandular organ.

Do the liver-cells, situated outside of the plexus of origin of the biliary duct, secrete the bile, which is taken up by these delicate vessels and carried to the excretory biliary passages? There are very good reasons for answering this question in the affirmative; although, if we do, we must recognize the fact that the same cells produce glycogenic matter. As far as we are able to understand the mechanism of secretion (except in the production of milk), it seems necessary that a formed anatomical element, known as a secreting cell, should elaborate, from materials furnished by the blood, the elements of secretion; and this cannot be accomplished by a structureless membrane like that which forms the walls of the bile-ducts. Under this view, assuming that bile, as bile, first makes its appearance in these little lobular tubes, the liver-cells are the only anatomical elements capable of producing the secretion. With regard to the mechanism of this secreting action, we have nothing to say beyond our general remarks in a previous chapter. With the view we have just expressed, certain elements of the bile are separated from the blood, and others are manufactured out of materials furnished by the blood by the liver-cells and are taken up by the delicate plexus of vessels situated between the cells. The discharge of the fluid is like the discharge of any other of the secretions, except that a portion is temporarily retained in a diverticulum from the main duct, the gall-bladder.

The two distinct functions of the liver now recognized by many physiologists, namely, the secretion of bile and the formation of sugar, have led to the question of the existence in the liver of two anatomically distinct portions or organs, corresponding to its double physiological function. This view, indeed, has been advanced by several eminent anatomists. Robin recognizes two distinct parts in the liver; a biliary organ and a glycogenic organ. He regards the lobules, with their liver-cells and blood-vessels, as the parts concerned in the glycogenic function of the liver, and the little glands which open into the biliary ducts all along their course (see Fig. 133) and are arranged on the duct "in the form of leaves of fern," as the biliary organ. The same independence of the glycogenic and biliary portions of the liver has been argued by others.

The fact that bile is found in the lobular canals and the demonstration of the direct communication of these canals with the excretory biliary ducts are powerful arguments in favor of the view that the bile is formed in the lobules, and probably by the liver-cells. What, then, is the function of the little acini connected exclusively with the biliary ducts? The similarity of their structure to that of the ordinary mucous glands, and to the mucous glands of the gall-bladder especially, would lead to the supposition that they secrete a mucous fluid. It is well known that the bile taken from the gall-bladder contains more mucus than that discharged directly from the liver; but the bile of the hepatic duct in most animals is somewhat viscid and contains a certain amount of mucus. This is the view entertained by Sappey, who states that the bile is viscid in different animals in proportion to the development of these little glands; and, in the rabbit, in which the glands do not exist, the bile is remarkably fluid.

Inasmuch as there is no direct evidence that the racemose glands attached to the excretory biliary passages have any thing to do with the secretion of the essential constituents of the bile, and as they are not even to be found in some animals that produce a considerable quantity of bile, we must regard the question of the isolation of two organs in the liver, one for the secretion of bile and the other for the production of sugar, as still unsettled. There is no evidence, indeed, that the bile is secreted anywhere but in the hepatic lobules.

Secretion of Bile from Venous or Arterial Blood.—Numerous experiments have been made with the view of determining whether the bile be secreted from the blood brought to the liver by the portal vein or from the blood of the hepatic artery. The immense quantity of blood distributed in the liver by the portal vein led first to the opinion that the impurities were separated from this blood to form the bile, and that the hepatic artery had little or nothing to do with the secretion. But, since Bernard discovered the glycogenic function of the liver, this subject has assumed additional importance; and it becomes a question whether the materials for the secretion of bile may not be furnished by one vessel (the hepatic artery), while the other (the portal vein) is specially concerned in the formation of glycogenic matter. This theoretical view, however, is not carried out by well-established anatomical facts or by physiological experiments. It is not yet possible to separate the liver anatomically into two organs, one for the secretion of bile and the other for the production of sugar. It seems certain, also, from numerous experiments, that bile may be secreted from the blood of the portal vein after a ligature has been applied to the hepatic artery; and it is equally certain, from the recent experiments of Oré, that, if the portal vein be obliterated so gradually that the animal does not die from the operation, bile is secreted from the blood of the hepatic artery. In support of this view, several instances of obliteration of the portal vein in the human subject are cited in works upon physiology. In a note to the communication of Oré in the *Comptes rendus*, Andral reports the case of a patient that died of dropsy, and on post-mortem examination the portal vein was found obliterated. In this instance the gall-bladder was found full of bile. In addition, instances in which the portal vein emptied into the vena cava have been reported, and in none was there any deficiency in the secretion of bile.

If the experiments upon the effects of tying the hepatic artery, and the observations of instances of obliteration of the portal vein and of congenital malformation, in which the portal vein does not go to the liver, be equally reliable, there is but one conclusion to be drawn from them; and that is, that bile may be secreted from either venous or arterial blood. This view is not inconsistent with what we know of the general process of secretion and its applications to the production of bile. Regarding the bile as in part an excrementitious fluid, its effete element, cholesterine, is contained both in the blood of the portal vein and the hepatic artery. Its recrementitious principles, glycocholates, taurocholates, etc., we suppose are produced *de novo* in the liver, out of materials furnished by the blood. The exact nature of the production of elements of secretion by glandular cells we do not understand; but there is no good reason to suppose that the principles necessary for the formation of bile may not be furnished by the blood of the portal vein, as well as by the hepatic artery.

The view most nearly in accordance with all the facts bearing on the question is, that bile is produced in the liver from the blood distributed in its substance by the portal vein and the hepatic artery, and not from either of these vessels exclusively; and that the bile may continue to be secreted, if either one of these vessels be obliterated, provided the supply of blood be sufficient.

Quantity of Bile.—The estimates of the daily quantity of bile in the human subject must be merely approximative; and our only ideas on this point are derived from experiments upon the inferior animals. The most complete and reliable observations upon this subject are those of Bidder and Schmidt, which were made upon animals with a fistula into the gall-bladder, the ductus communis having been tied. These observers found great variations in the daily quantity in different classes of animals, the quantity in the carnivora being the smallest. Applying their results to the human subject, assuming that the amount is about equal to the quantity secreted by the carnivora, the daily secretion in a man weighing one hundred and forty pounds would be about two and a half pounds.

Variations in the Flow of the Bile.—We have already considered, under the head of digestion, the variations in the flow of bile and their relation to the process of intestinal digestion. It is sufficient in this connection to repeat that the discharge from a biliary fis-
tula in a dog increases immediately after eating; that it is at its maximum from the second
to the eighth hour, during which time it does not vary to any great extent; after the eighth
hour it begins to diminish; and, from the twelfth hour to the time of feeding, it is at its
minimum. These facts show that, while the bile is discharged much more abundantly
during intestinal digestion than during the intervals of digestion, its production and dis-
charge are constant. This, as we shall see farther on, is a strong argument in favor of
the view that the liver has an excrementitious function.

The bile is stored up in the gall-bladder to a considerable extent during the intervals of digestion. If an animal be killed at this time, the gall-bladder is always distended; but it is found empty, or nearly so, in animals killed during digestion.

The influence of the nervous system upon the secretion of bile has been very little studied, and the question is one of great difficulty and obscurity. The liver is supplied very abundantly with nerves, both from the cerebro-spinal and the sympathetic system, and some observations have been made upon the influence of the nerves upon its glycogenic function; but, with regard to the secretion of bile, we can only apply our general remarks concerning the influence of the nervous system on secretion.

The bile is discharged through the hepatic ducts like the secretion of any other gland. During digestion, the fluid accumulated in the gall-bladder passes into the ductus communis, in part by contractions of its walls, and in part, probably, by compression exerted by the distended and congested digestive organs adjacent to it. It seems that this fluid, which is necessarily produced by the liver without intermission, separating from the blood certain excrementitious matters, is retained in the gall-bladder for use during digestion.

Functions of the Bile.

Although the function of the bile in intestinal digestion is essential to life, we know very little of its mode of action; and we have thought proper to defer until now a full consideration of the properties and composition of this secretion. For an account of what is known of its digestive function, the reader is referred to the chapters treating of digestion. We shall show, in this connection, that the liver excretes one of the most important of the effete principles; but, before taking up the relations of the bile as an excretion, it will be necessary to study its general properties and composition.

General Properties of the Bile.—The secretion, as it comes directly from the liver, is somewhat viscid; but, after it has passed into the gall-bladder, its viscidity is much increased from a farther admixture of mucus.

The color of the bile is very variable within the limits of health. It may be of any shade between a dark, yellowish-green and a reddish-brown. It is semitransparent, except when the color is very dark. In different classes of animals, the variations in color are very great. In the pig it is bright-yellow; in the dog it is dark-brown; and in the ox it is greenish-yellow. As a rule, the bile is dark-green in the carnivora and greenish-yellow in the herbivora.

The specific gravity of the human bile is from 1020 to 1026. When the bile is perfectly fresh, it is almost inodorous, but it readily undergoes putrefactive changes. It has an excessively disagreeable and bitter taste. It is not coagulated by heat. When mixed with water and shaken, it becomes frothy, probably on account of the tenacious mucus and its saponaceous constituents.

It is generally stated that the bile is invariably alkaline. This is true of the fluid discharged from the hepatic duct, although the alkalinity is not strongly marked; but the reaction varies after it has passed into the gall-bladder. Bernard found it sometimes acid and sometimes alkaline in the gall-bladder, in animals (dogs, and rabbits) killed under various conditions; but many of these animals were suffering from the effects of severe operations. In the hepatic ducts the reaction is always alkaline; and there are no observations on human bile that show that the fluid is not alkaline in all of the biliary passages.

We have already noted the fact that the epithelium of the biliary passages is strongly tinged with yellow, even in living animals. This is due to the remarkable facility with which the coloring principle of the bile stains the animal tissues. This is very well illustrated in icterus, when even a small quantity of this coloring matter finds its way into the circulation.

Perfectly normal and fresh bile, examined with the microscope, presents a certain amount of mucus, the characters of which we have already described. There are no formed anatomical elements characteristic of this fluid. The fatty and coloring matters are in solution and not in the form of globules or granules.

Composition of the Bile.

It is a remarkable fact, that, although the bile, in a perfectly fresh and normal condition, may be obtained from the inferior animals with the greatest facility, no satisfactory analyses of its characteristic principles were made before the examinations of ox-gall by Strecker, in 1848. The bile is, however, one of the most important, but least understood, of the animal fluids; and our scanty information with regard to its functions has been in a measure due to the want of an exact knowledge of its physiological chemistry. We shall study the composition of the bile very closely, and shall show that it contains two classes of constituents: one class—elements of secretion—which is reabsorbed; and another—an element of excretion—which is discharged in a modified form in the fæces. The latter involves a newly-described function of the liver, but our information is much more positive and definite concerning it than with regard to the digestive action of the bile. In treating of the subject of digestion, we have already indicated some of the difficulties, which have been but imperfectly overcome, in the study of the action of the bile as a true secretion, or a recrementitious fluid. The reason why the same obscurity has prevailed with regard to the function of the bile as an excretion is that physiologists have regarded what are known as the biliary salts as the only really important constituents; and these salts have eluded chemical investigation after the discharge of the bile into the small intestine. Our recent positive knowledge of the excrementitious function of the liver is due to the recognition of cholesterine, an invariable constituent of the bile, as one of the most important of the elements of excretion.

Composition of Human Bile. (Robin.)

Water	916·00 to 819·00
Taurocholate, or choleate of soda	56·50 " 106·00
Glycocholate, or cholate of soda	traces.
Cholesterine	0·62 to 2·66
Biliverdine	14·00 " 30·00
Lecithene; Margarine, oleine, and traces of soaps	3·20 " 31·00
Choline	traces.
Chloride of sodium	2·77 to 3·50
Phosphate of soda	1·60 " 2·50
Phosphate of potassa	0·75 " 1·50
Phosphate of lime	0·50 " 1·35
Phosphate of magnesia	0·45 " 0·80
Salts of iron	0·15 " 0·30
Salts of manganese	traces " 0·12
Silicic acid	0·03 " 0·06
Mucosine	traces.
Loss	3·43 to 1·21
	1,000·00 1,000·00

There are no peculiarities in the composition of the bile, as regards its inorganic constituents, which demand more than a passing mention. It contains no coagulable organic principle, except mucosine, and all of its constituents are simply solids in solution. The quantity of solid matter is very large, and the proportion of water is relatively small; but, in comparing its proportion of water with that of other fluids in the body, as the blood-plasma, lymph and chyle, milk, etc., it must be remembered, as is suggested by Robin, that all of these contain water entering into the composition of their coagulable principles; so that their proportion of water, as it is ordinarily given, is really not greater than in the bile. Among the inorganic salts, we find chloride of sodium in considerable quantity and a large proportion of phosphates. We also note the presence of salts of iron, of manganese, and a small proportion of silicic acid.

The fatty and saponaceous matters demand hardly any more extended consideration. A small quantity of margarine and oleine are held in solution, partly by the small proportion of soaps, but chiefly by the taurocholate of soda. These principles sometimes exist in larger quantity, when they may be discovered in the form of globules. The proportion of soaps is very small. Lecithene, a phosphorized fat, is mentioned by Robin and others, but its constitution is not definitely settled. All that is known of this principle is that it is a neutral fatty substance extracted from the bile, and is capable of being decomposed into phosphoric acid and glycerine. Choline is a peculiar alkaloid found in the bile in exceedingly minute quantity.

Biliary Salts.—The principles which we have called biliary salts are compounds of soda with peculiar organic acids, found nowhere but in the liver, and undoubtedly produced in this organ from materials furnished by the blood. The fact that the bile possesses peculiar principles has long been recognized. It is unnecessary, however, to follow out in detail the earlier chemical investigations into their properties; for the biliary matter of Berzelius and the picromel and biliary resin of Thenard are now known to be composed of several distinct proximate principles. Our exact knowledge of these substances dates from the analyses of ox-bile by Strecker. He obtained two peculiar acids, cholic and choleic acid, which he found in the bile, in combination with soda. In the subsequent researches of Lehmann, these acids are called, respectively, glycocholic and taurocholic acid, and the salts, glycocholate and taurocholate of soda.

In human bile, the proportion of glycocholate of soda is very small, the biliary matter existing almost entirely in the form of the taurocholate. The taurocholate may be precipitated from an alcoholic extract of bile by ether, in the form of dark, resinous drops. These do not crystallize, and the amount of glycocholate, which is precipitated in the same way and soon assumes a crystalline form, is very slight. Prof. Dalton, who has studied the biliary salts very closely, at first was unable to obtain any crystalline matter from human bile, but he has lately found it in minute quantity.

Taurocholate of Soda.—There is some doubt whether the resinous drops obtained by the addition of an excess of ether to a strong alcoholic extract of bile consist of a proximate principle in a perfectly pure state. These drops are not crystallizable, and this has led to the opinion that they are impure. In fact, even now, there is a certain amount of obscurity with regard to the character of these peculiar biliary salts. In ox-bile, the non-crystallizable and the crystallizable salts exist together; but, in human bile, the greatest part is in the form of what we know as the taurocholate of soda.

These salts may be readily obtained from ox-bile and separated from each other by the following process: The bile is first evaporated to dryness and pulverized. The dry residue is then extracted with absolute alcohol and filtered. In this part of the process, Dr. Dalton uses five grains of the dry residue to one fluidrachm of alcohol. The filtered fluid is of a clear, yellowish color, and it contains fats and coloring matter, in addition to the biliary salts. To precipitate the biliary salts, a small quantity of ether is added, which produces a dense, white precipitate that redissolves by agitation. Another small quantity of ether is again added, and the precipitate thus produced is dissolved by shaking the mixture. This process is repeated carefully, adding the ether and shaking the mixture after each step, until the precipitate becomes permanent. An excess of ether—from eight to ten times the bulk of the alcoholic extract used—is then added, the test-tube or flask is carefully corked, and the mixture is set aside to crystallize. Gradually the dense, white precipitate falls to the bottom of the vessel or becomes attached in the form of resinous drops to the sides of the glass; and in from six to twenty-four hours it begins to form delicate, acicular crystals, arranged in rosettes. These are crystals of the glycocholate of soda; and the non-crystallizable matter remaining is the taurocholate of soda.

To separate the biliary salts from each other, the ether is rapidly poured off, and the crystalline and resinous residue is dissolved in distilled water. On the addition to this solution of a little acetate of lead, the glycocholate is decomposed and precipitated in the form of glycocholate of lead, leaving the taurocholate in solution. The glycocholate of lead is then separated by filtration, and the subacetate of lead is added to the filtered fluid. This decomposes the taurocholate, and the taurocholate of lead is precipitated. The subacetate of lead will decompose both the glycocholate and the taurocholate, but the glycocholate only is acted upon by the acetate of lead. The glycocholate and the taurocholate of lead are then carefully washed and treated separately with the carbonate of soda, which gives the original salts in nearly a pure state.

The taurocholate of soda is a proximate principle of the bile; and it is not necessary to describe fully in detail the purely chemical processes by which it is decomposed. With a little care, the taurocholic acid may be obtained in a state of tolerable purity, and, by prolonged boiling with potash, it may be decomposed into a new acid and taurine. Some confusion exists in the books about the name of this new acid. Strecker calls it choleic acid, and he applies the name of cholic acid to what we have described as glycocholic acid. As we have adopted the nomenclature of Lehmann, we shall call it cholic acid. It must be remembered, however, that these substances are formed artificially and are not true proximate principles. They have been described in explanation of the name taurocholic acid, which has been applied to this acid on the assumption that the different biliary acids are formed of cholic acid united with taurine or other basic substances.

If human bile be treated in the manner just described, frequently no crystalline matter is obtained, and, when it exists, it is in very small quantity. The great mass of the precipitate is composed of the taurocholate of soda. This, when it has been thoroughly

FIG. 135.—*Crystals of glycocholate of soda; magnified* 100 *diameters.* (Robin.)

purified, is whitish and gummy, very soluble in water and alcohol, and insoluble in ether. It is melted with slight heat and is inflammable. Its reaction is neutral. It has a peculiar sweetish-bitter taste. The proportion of this principle in the bile is always very large, although it is subject to considerable variation. It has very little in common with the salts of fatty origin, either in its general properties or composition, inasmuch as it is entirely insoluble in ether, and its acid contains nitrogen. Another peculiarity in its composition, and one which serves to distinguish it from the glycocholate of soda, is that it contains two atoms of sulphur. One of its important properties in the bile is that it aids in the solution of the fats contained in this fluid, and to a certain extent, probably, in the solution of cholesterine.

Glycocholate of Soda.—We have necessarily described the process for the extraction of the glycocholate of soda, in connection with the taurocholate. The glycocholate is crystallizable and is more easily obtained in a condition of purity. The chemical points of difference between these salts are, that the glycocholate is precipitated by the acetate of lead as well as the subacetate, the acetate having no effect upon the taurocholate of soda, and that the glycocholic acid does not contain sulphur. By treating glycocholic acid with potash at a high temperature, it is decomposed into cholic acid and glycine, or glycocoll. It is this which has given it the name of glycocholic acid. In their physiological relations, the two biliary salts are, as far as we know, identical.

Origin of the Biliary Salts.—There can be no doubt that these principles are elements of secretion and are produced *de novo* in the substance of the liver. In no instance have they ever been discovered in the blood in health; and, although they present certain points of resemblance with some of the constituents of the urine, they have never been found in the excreta. In experiments made by Müller, Kunde, Lehmann, and Moleschott, on frogs, in which the liver was removed and the animal survived several days, and, in the observations of Moleschott, between two and three weeks, it was found impossible to determine the accumulation of the biliary salts in the blood. There is no reason, therefore, for supposing that these principles are products of disassimilation. Once discharged into the intestine, they undergo certain changes and can no longer be recognized by the usual tests; but experiments have shown that, changed or unchanged, they are absorbed with the elements of food. They are probably the elements concerned in the digestive function of the bile.

Cholesterine.—Before the publication, in 1862, of a memoir on a new excretory function of the liver, the function and relations of cholesterine were not known, and this substance was hardly mentioned in most works on physiology. As we believe that it must now be recognized as one of the most important of the products of disassimilation, it becomes interesting and important to study its properties more closely.

Cholesterine is now recognized as a normal constituent of various of the tissues and fluids of the body. Most authors state that it is found in the bile, blood, liver, nervous tissue, crystalline lens, meconium, and fæcal matter. We have found it in all these situations, with the exception of the fæces, where it does not exist normally, being transformed into stercorine in its passage down the intestinal canal.

In the fluids of the body, cholesterine exists in solution; but by virtue of what constituents it is held in this condition, is a question that is not entirely settled. It is stated that the biliary salts have the power of holding cholesterine in solution in the bile, and that the small amount of fatty acids contained in the blood holds it in solution in that fluid; but direct experiments on this point are wanting. In the nervous substance and in the crystalline lens, it is united "*molecule à molecule*" to the other elements which go to make up these tissues. After it is discharged into the intestinal canal, when it is not changed into stercorine, it is to be found in a crystalline form, as in the meconium and in the fæces of animals in a state of hibernation. In pathological fluids and in tumors, it is found in a crystalline form and may be detected by microscopical examination.

Cholesterine is usually described as a non-nitrogenized principle, having all the properties of the fats, except that of saponification with the alkalies. It is neutral, inodorous, crystallizable, insoluble in water, soluble in ether, very soluble in hot alcohol, though sparingly soluble in cold alcohol. It is inflammable and burns with a bright flame. It is not attacked by the alkalies, even after prolonged boiling. When treated with strong sulphuric acid, it strikes a peculiar red color, which is mentioned by some as characteristic of cholesterine. We have found that it possesses this character in common with the so-called seroline.

Cholesterine may easily and certainly be recognized by the form of its crystals, the characters of which can be made out by means of the microscope. They are rectangular or rhomboidal, exceedingly thin and transparent, of variable size, with distinct and generally regular borders, and frequently are arranged in layers, with the borders of the lower strata showing through those which are superimposed. This arrangement of the crystals takes place when cholesterine is present in considerable quantity. In pathological specimens, the crystals are generally few in number and isolated. The plates of cholesterine are frequently marked by a cleavage at one corner, the lines running parallel to the borders; and frequently they are broken, and the line of fracture is generally undulating. Frequently the plates are rectangular, and sometimes they are almost lozenge-shaped. It is by the transparency of the plates, the parallelism of their borders, and their tendency to break in parallel lines, that we recognize cholesterine. Crystals of cholesterine melt at 293° Fahr., but they are formed again when the temperature falls below that point. The determination of the fusing-point is one of the means of distinguishing cholesterine from seroline, which latter fuses at 90° 8′.

FIG. 136.—*Cholesterine extracted from the bile; 1/5 inch objective.*

Without considering in detail the processes which have been employed by other observers for the extraction of cholesterine from the blood, bile, and various tissues of the body, we shall simply describe the method which has been found most convenient in the various analyses we have made for this substance. In analyses of gall-stones, the process is very simple; all that is necessary being to pulverize the mass, extract it with boiling alcohol, and filter the solution while hot, the cholesterine being deposited on cooling. If the crystals be colored, they may be redissolved and filtered through animal charcoal. It is only when this substance is mixed with fatty matters, that its isolation is a matter of any difficulty. In extracting cholesterine from the blood, we have operated on both the serum and clot, and, in this way, we have been able to demonstrate it in greater quantities in this fluid than have been observed by others, who have employed only the serum. The following is the process for quantitative analysis, which was fixed upon after a number of experiments:

The blood, bile, or brain, as the case may be, is first carefully weighed, then evaporated to dryness over a water-bath, and afterward pulverized in an agate mortar. The powder is then treated with ether, in the proportion of about a fluidounce for every hundred grains of the original weight, for from twelve to twenty-four hours, agitating the mixture occasionally. The ether is then separated by filtration, throwing a little fresh ether on the filter so as to wash through every trace of the fat, and the solution is set aside to evaporate. If the fluid, especially the blood, have been carefully dried and pulverized, when the ether is added it divides it into a very fine powder and penetrates every part. After the ether has evaporated, the residue is extracted with boiling alcohol, in the proportion of about a fluidrachm for every hundred grains of the original weight of the specimen, filtered while hot into a watch-glass, and allowed to evaporate spontaneously. To keep the fluid hot while filtering, the whole apparatus may be placed in the chamber of a large water-bath, or, as the filtration is generally rapid, the funnel may be warmed by plunging it into hot water, or steaming it, taking care that it be carefully wiped. We now have the cholesterine mixed with a certain quantity of saponifiable fat. After the fluid has evaporated, we can see the cholesterine crystallized in the watch-glass, mingled with masses of fat. This we remove by saponification with an alkali; and, for this purpose, we add a moderately strong solution of caustic potash, which we allow to remain in contact with the residue for one or two hours. If much fat be present, it is best to heat the mixture to a temperature a little below the boiling-point; but in analyses of the blood this is not necessary. The mixture is then to be largely diluted with distilled water, thrown upon a small filter, and thoroughly washed till the fluid which passes through is neutral. We then dry the filter and fill it up with ether, which, in passing through, dissolves out the cholesterine. The ether is then evaporated, the residue extracted with boiling alcohol as before, the alcohol collected on a watch-glass previously weighed, and allowed to evaporate. The residue consists of pure cholesterine, the quantity of which may be estimated by weight.

The accuracy of this process may be tested by means of the microscope; for the crystals have so distinctive a form that it is easy to determine, by examining the watch-glass, that the cholesterine is perfectly pure. In making this analysis quantitatively, it is necessary to be very careful in all the manipulations; and, for determining the weight of such minute quantities, an accurate and delicate balance, one, at least, that will turn with the thousandth of a gramme, carefully adjusted, must be employed. With these precautions, the quantity of cholesterine in any fluid or solid may be determined with perfect accuracy; and the estimate may be made in a quantity of blood not exceeding fifteen or twenty grains. In analyzing the brain and bile, we found it necessary to pass the first ethereal solution through animal charcoal, in order to get rid of the coloring matter. In doing this, the charcoal must be washed with fresh ether until the solution which passes through is brought up to the original quantity. The other manipulations are the same as in the analyses of the blood. In examining the meconium, we found that the cholesterine which crystallized from the first alcoholic extract was so pure that it was not necessary to subject it to the action of an alkali.

The proportion of cholesterine in the bile is not very large. In the table, it is estimated at from 0·62 to 2·66 parts per thousand. In a single examination of the human bile, we found the proportion 0·618 of a part per thousand.

The origin and destination of this principle involve, as we believe, an office of the liver which has not hitherto been recognized by physiologists; and we shall consider these questions specially, under the head of the excretory function of the liver.

Biliverdine.—The coloring matter of the bile bears a certain resemblance to the coloring matter of the blood and is supposed to be formed from it in the liver. It gives to the bile its peculiar tint, and has, as we have remarked, the property of coloring the tissues with which it comes in contact. Whenever the flow of bile is seriously obstructed, the coloring matter is absorbed by the blood, and it can be readily detected in the serum and in the urine. It also colors the skin and the conjunctiva. In the bile it is liquid, but it may be coagulated and extracted by various processes. It does not exist naturally in the form of pigmentary granulations.

This principle is precipitated from the bile by boiling with milk of lime. The filtered residue is then decomposed with hydrochloric acid, which unites with the lime and leaves a fatty residue, of an intense-green color. The fat is then removed by repeated washings with ether, which is a very long and difficult process. The precipitate is then redissolved in alcohol with ether added, which gives to the liquid a bluish-green color, and leaves, after evaporation, a dark-green powder. This powder contains iron, but its proportion has never been accurately estimated. The matter thus obtained is insoluble in water and in chloroform, but it is soluble in ether, alcohol, sulphuric and hydrochloric acid.

It is unnecessary to follow out in detail all of the chemical investigations which have been made into the ultimate composition and the modifications of this and the other coloring matters. Recent researches have shown that, in all probability, the coloring matter called biliverdine is a mixture of several distinct coloring principles, and that these rapidly change in contact with the oxygen of the air; so that there is considerable uncertainty with regard to the ultimate composition of these and other substances of the same class.

Tests for Bile.—It is frequently desired, particularly in pathological investigations, to ascertain, by some easy test, the fact of the presence or absence of bile in various of the fluids and solids of the body. It is, indeed, a most interesting physiological question to determine the course and destination of the biliary salts after the bile has passed into the intestinal canal; and this can be done only by the application of appropriate tests to the contents of the alimentary tract and the blood of the portal system. The ingredients of the bile which it is important to detect are biliverdine, the biliary salts, and cholesterine. The last-named substance can be detected most readily by applying the method which we have just described for its extraction; but several tests have been proposed for the detection, on the one hand, of the coloring matter of the bile, and, on the other, of the peculiar biliary salts.

Test for Biliverdine.—There is one test so simple and easy of application, that it alone will suffice for the prompt detection of biliverdine. This is peculiarly applicable to the urine, where the presence or absence of bile frequently becomes an important question.

We are led generally to suspect the presence of bile in the fluids of the body by their peculiar color. If we spread out the suspected fluid in a thin stratum upon a white surface, as a porcelain plate, and add a single drop of nitric acid, or, what is better, nitroso-nitric acid, if the coloring matter of bile be present, a peculiar play of colors will be observed at the circumference of the drop of acid as it diffuses itself. The color will rapidly change from blue to red, orange, purple, and finally to yellow. This is due to the action of the acid upon the biliverdine; and this test does not indicate the presence of either cholesterine or the biliary salts. It is used, therefore, only when we wish to determine the presence of the coloring matter of the bile.

Test for the Biliary Salts.—The best, and, indeed, the only reliable test for the biliary salts, was proposed many years ago by Pettenkofer, and this is now generally known as Pettenkofer's test. This requires some care and practice in its application, but it is entirely reliable; and, although it has been objected that there are other substances, beside the biliary salts, which produce similar reactions, they are not met with in the animal fluids and consequently are not liable to produce confusion. If a considerable quantity of bile be present in any fluid, and if there be not a large admixture of animal matters, the test may be employed without any previous preparation; but, in delicate examinations, it is best to evaporate the suspected liquid, extract the residue with absolute alcohol, precipitate with ether, and dissolve the ether-precipitate in distilled water. By this means a clear solution is obtained, which will react distinctly, even when the biliary salts exist in very small quantity. Pettenkofer's test is applicable to any of the biliary salts, whatever be their form, and the reaction is dependent upon the presence of cholic acid, which enters into the composition of all the varieties of the biliary acids.

The following is one of the most common methods of employing Pettenkofer's test: To the suspected solution we add a few drops of a strong solution of cane-sugar in water. Sulphuric acid is then slowly added, to the extent of about two-thirds of the bulk of the liquid. It is recommended to add the acid slowly, so that the temperature shall be but little raised. If a large quantity of the biliary salts be present, a red color shows itself almost immediately at the bottom of the test-tube, and this soon extends through the entire liquid, rapidly deepening until it becomes of a dark-lake or purple. If the biliary matters exist in very small proportion, it may be several minutes before any red color makes its appearance, and the change to a purple is correspondingly slow, the whole process occupying from fifteen to twenty minutes. Many organic matters may be rendered dark by the action of the acid, and the sugar itself will be acted upon, even if no bile be present, but the color due to the sugar alone is yellow. The peculiar play of colors above described can easily be recognized after a little practice, and is observed only in the presence of the biliary salts.

The ordinary modifications in the application of this test are unimportant. Some recommend to add the sulphuric acid first, and then to add the solution of sugar; and some, after adding to the liquid two-thirds of its volume of sulphuric acid, drop into the mixture one or two lumps of cane-sugar. The reaction with the biliary salts is essentially the same, whichever of these methods be employed.

Excretory Function of the Liver.

In 1862, in studying the properties and physiological relations of cholesterine, we gave the first definite account of an excretory function of the liver. The experiments and observations upon which we based our conclusions were extended and laborious, and, as far as we know, they have not been repeated in detail by other observers; but the results must be taken as positive, if the accuracy of the experiments be admitted, and they have been adopted, to a greater or less extent, by scientific authorities. The details of these experiments are too elaborate to be given in full, as contained in the original memoir.[1]

The few statements with regard to the function of cholesterine to be found in works published before 1862 are very indefinite. In most treatises on physiology, this substance is hardly mentioned, it being generally regarded as a curious principle, interesting only to the physiological chemist. We have given, in the memoir referred to, extracts from the works of Carpenter, Lehmann, Mialhe, and Dalton, which contain all that is said with regard to the probable function of cholesterine; and these quotations, which embody about all that we could find on the subject, show that its office was not in the least understood. Inasmuch as cholesterine is the only excrementitious principle as yet discovered in the bile, bearing the same relation to this fluid that urea does to the urine, it is evident that the ideas of physiologists, with regard to any excretory function of the liver, must have been very indefinite before the relations of cholesterine had been determined.

The first question which arises is whether the liver has any excretory function. Some authors have assumed that the bile is purely excrementitious and has no function as a secretion. This question we have fully discussed in connection with the subject of digestion. The confusion that has arisen with regard to this point has been due to the fact that those who adopted the view that the bile was simply an excretion denied to it any digestive properties; while, on the other hand, those who believed it to be concerned in digestion would not admit that it was an excretion. We have shown conclusively, in treating of intestinal digestion, that the bile is so important in this process as to be essential to life; but we have shown, at the same time, that the liver eliminates from the blood one of the most important of the products of disassimilation. It will be found important, as bearing upon the probable function of the bile, to apply to this fluid the general law of the distinctions between secretions and excretions.

Cells of glandular epithelium are constantly manufacturing, out of materials furnished by the blood, the elements of the true secretions; but these elements do not preëxist in the blood, they appear *de novo* in the secreting organ, and they never accumulate in the system when the function of the secreting organ is disturbed. Again, the true secretions are not discharged from the body, but they have a function to perform in the economy, and are poured out by the glands intermittently, at the times when this function is called into action. As far as the biliary salts (the taurocholate and glycocholate of soda) are concerned, the bile corresponds entirely to the true secretions. These principles are manufactured by the liver, they do not preëxist in the blood, and they do not accumu-

[1] Flint, Jr., *Experimental Researches into a New Excretory Function of the Liver.—American Journal of the Medical Sciences*, Philadelphia, 1862, New Series, vol. xliv., p. 305, *et seq.*; and, *Recherches expérimentales sur une nouvelle fonction du foie*, Paris, 1868.

late in the blood when their formation in the liver is disturbed. The researches of Bidder and Schmidt and others have shown that, although we cannot detect the biliary salts in the blood or chyle coming from the intestine, these principles are not discharged in the fæces. All of these facts point to an important function of the bile as a secretion. It is true that it is discharged constantly, but, during digestion, its flow is very much more abundant than at any other time. It is pretty well established that, during the intervals of the flow of the secretions, the glands are manufacturing the materials of secretion, which are washed out, as it were, in the great afflux of blood which takes place during what has been called the functional activity of the gland. Now, if the liver, in addition to its function as a secreting organ, be constantly forming bile for the purpose of eliminating an excrementitious matter, it is to be expected that the bile would always contain a certain proportion of its elements of secretion.

The constant and invariable presence of cholesterine in the bile assimilates it in every regard to the excretions, of which the urine may be taken as the type. Cholesterine always exists in the blood and in certain of the tissues of the body. It is not produced in the substance of the liver, but is merely separated from the blood by this organ. It is constantly passed into the intestine, and is discharged, although in a modified form, in the fæces. We know of no function which it has to perform in the economy, any more than urea or any other of the excrementitious principles of the urine; and we have shown, in the memoir already referred to, that it accumulates in the blood in certain cases of organic disease of the liver and gives rise to symptoms of blood-poisoning.

Origin of Cholesterine.—Cholesterine exists in largest quantity in the substance of the brain and nerves. It is also found in the substance of the liver—probably in the bile contained in this organ—the crystalline lens, and the spleen; but, with these exceptions, it is found only in the nervous system and blood. Two views present themselves with regard to its origin. It is either deposited in the nervous matter from the blood, or it is formed in the brain and taken up by the blood. This is a question, however, which can be settled experimentally, by analyzing the blood for cholesterine as it goes to the brain by the carotid and as it comes from the brain by the internal jugular. The cholesterine being found also in the nerves, and, of course, a large quantity of nervous matter existing in the extremities, it is desirable at the same time to make an analysis of the venous blood from the general system.

With a view of determining this question, we made the following experiments:

Experiment I.—In this experiment, specimens of blood were taken from the carotid, the internal jugular, the vena cava, hepatic veins, hepatic artery, and portal vein, in a living animal (a dog about six months old). In addition, we took a specimen of bile from the gall-bladder, and some of the substance of the brain. These were all carefully examined for cholesterine, and the following were the main results: In the brain, cholesterine was found in large quantity. There was no cholesterine in the extract of the blood from the carotid, examined three days after, and but a few crystals, eleven days after. Cholesterine was almost immediately discovered in the extract of the blood from the internal jugular, and the crystals were present in large numbers on the twelfth day. In this experiment, the animal was etherized when the blood was taken, and the examinations for cholesterine were not quantitative. In the succeeding experiments, the proportion of cholesterine in the different specimens of blood was accurately estimated, and, in most of them, no anæsthetic was used during the operative procedure.

Experiment II.—A medium-sized adult dog was put under the influence of ether, and the carotid artery, internal jugular, and femoral vein exposed. Specimens of blood were drawn, first from the internal jugular, next from the carotid, and last from the femoral vein. These specimens were received into carefully-weighed vessels, and weighed. They were then analyzed for cholesterine by the process already described, with the following results:

	Quantity of blood. *grains.*	Cholesterine. *grains.*	Cholesterine per 1,000 pts.
Carotid	179·462	0·139	0·774
Internal jugular	134·780	0·108	0·801
Femoral vein	133·886	0·108	0·806

Percentage of increase in the blood from the jugular over the arterial blood .... 3·488
Percentage of increase in the blood from the femoral vein over the arterial blood .... 4·134

This experiment shows an increase in the quantity of cholesterine in the blood in its passage through the brain, and an increase, even a little greater, in the blood passing through the vessels of the posterior extremity. To facilitate the operation, however, the animal was brought completely under the influence of ether, which, from its action upon the brain, would not improbably produce some temporary disturbance in the nutrition of that organ, and consequently might interfere with the experiment. For the purpose of avoiding this difficulty, we performed the following experiments without administering an anæsthetic:

Experiment III.—A small, young dog was secured to the operating-table, and the internal jugular and carotid were exposed upon the right side. Blood was taken, first from the jugular, and afterward from the carotid. The femoral vein upon the same side was then exposed, and a specimen of blood was taken from that vessel. The animal was very quiet under the operation, although no anæsthetic was used, so that the blood was drawn without any difficulty and without the slightest admixture.

The three specimens were analyzed for cholesterine, with the following results:

	Quantity of blood. *grains.*	Cholesterine. *grains.*	Cholesterine per 1,000 pts.
Carotid	143·625	0·679	0·967
Internal jugular	29·956	0·046	1·545
Femoral vein	45·035	0·046	1·028

Percentage of increase in the blood from the jugular over the arterial blood .... 59·772
Percentage of increase in the blood from the femoral vein over the arterial blood .... 6·308

Experiment IV.—A large and powerful dog was secured to the operating-table, and the carotid and internal jugular were exposed. Specimens of blood were taken from these vessels, first from the jugular, and were carefully weighed and analyzed for cholesterine in the usual way. The following results were obtained:

	Quantity of blood. *grains.*	Cholesterine. *grains.*	Cholesterine per 1,000 pts.
Carotid	140·847	0·108	0·768
Internal jugular	97·811	0·092	0·947

Percentage of increase in the blood passing through the brain .... 23·307

Experiment III. shows a very considerable increase in the quantity of cholesterine in the blood passing through the brain, while the increase is comparatively slight in the blood of the femoral vein. The proportion of cholesterine is also large in the arterial blood, as compared with other observations.

Experiment IV. shows but a slight difference in the quantity of cholesterine in the arterial blood in the two animals; the proportion in the animal that was etherized being 0·774 per 1,000, and in the animal that was not etherized, 0·768 per 1,000, the difference being but 0·006; but, as was suspected, the ether seemed to have an influence upon the quantity of cholesterine absorbed by the blood in its passage through the brain. In the first instance the increase was but 3·488 per cent., while in the latter it was 23·307 per cent.

The natural conclusions to be drawn from these observations, with regard to the origin of cholesterine in the economy, are the following: It has been ascertained that the brain and nerves contain a large quantity of this substance, which is found in hardly any other of the tissues of the body; and these experiments, especially Experiments III. and IV., show that the blood that comes from the brain contains a much larger quantity of cholesterine than the blood supplied to this organ.

The conclusion is, then, that cholesterine is produced in the brain and is taken up by the blood as it passes through this organ.

But the brain is not the only part where cholesterine is produced. It will be seen by Experiment II. that there is 4·134 per cent., and in Experiment III., 6·308 per cent. of increase in cholesterine in the passage of the blood through the inferior extremities, and probably about the same in other parts of the muscular system. In examining these tissues chemically, we find that the muscles contain no cholesterine, but that it is abundant in the nerves; and, as we have found that the proportion of cholesterine is immensely increased in the passage of the blood through the great centre of the nervous system, taken, as the specimens were, from the internal jugular, which collects the blood mainly from the brain and very little from the muscular system, it is very probable that, in the general venous system, the cholesterine which the blood contains is produced in the substance of the nerves.

If the above conclusion be correct, and if cholesterine be one of the products of the disassimilation of nervous tissue, its formation would be proportionate in activity to the nutrition of the nerves; and any thing which interfered to any great extent with their nutrition would diminish the quantity of cholesterine produced. In the production of urea by the general system, which is analogous to the formation of cholesterine, muscular activity increases the quantity, and inaction diminishes it, on account of their influence upon nutrition. In cases of paralysis, we have a diminution of the nutritive forces in the parts affected, especially of the nervous system, which, after a time, becomes so disorganized that, although the cause of the paralysis be removed, the nerves cannot resume their functions. It is true that we have this disorganization taking place to a certain extent in the muscles, but this is by no means so marked as it is in the nerves. We should be able, then, to confirm the observations on animals by examining the blood in cases of paralysis, when we should expect to find a very marked difference in the quantity of cholesterine, between the venous blood coming from the paralyzed parts and the blood from other parts of the body. With this point in view, we made analyses of the blood from both arms, in three cases of hemiplegia:

Case I.—Sarah Rumsby, æt. 47, was affected with hemiplegia of the left side. Two years ago she was attacked with apoplexy and was insensible for three days. When she recovered consciousness, she found herself paralyzed on the left side. She said she had epilepsy four or five years before the attack of apoplexy. Now she has entire paralysis of motion of the affected side, with the exception of some slight power over the fingers, but sensation is perfect. The speech is not affected. The general health is good.

Case II.—Anna Wilson, æt. 23, Irish, was affected with hemiplegia of the right side. Four months ago she was attacked with apoplexy, from which she recovered in one day, with loss of motion and sensation of the right side. She is now improving and can use the right arm slightly. The leg is not so much improved, because she will make no effort to use it.

Case III.—Honora Sullivan, æt. 40, Irish, was affected with hemiplegia of the right side. About six months ago she was attacked with apoplexy and recovered consciousness the next day, with paralysis. The leg was less affected than the arm, from the first. The cause was supposed by Dr. Austin Flint, the attending physician, to be due to an embolus. Her condition is now about the same as regards the arm, but the leg has somewhat improved.

These cases all occurred at the Blackwell's Island Hospital. The treatment in all consisted of good diet, frictions, passive motion, and use of the paralyzed members as much as possible.

A small quantity of blood was drawn from both arms in these three cases. It was drawn from the paralyzed side, in each instance, with great difficulty, and but a small quantity could be obtained.

The specimens were all examined for cholesterine, with the following results:

Table of Quantities of Cholesterine in Blood of Paralyzed and Sound Sides, in Three Cases of Hemiplegia.

	Blood.	Cholesterine.	Cholesterine per 1,000.
	Grains.	Grains.	
Case I. Paralyzed side.	55·458	....	The watch-glass contained 0·031 of a grain of a granular substance, but the most careful examination failed to reveal a single crystal of cholesterine.
Do. Sound side...	128·407	0·062	0·481.
Case II. Paralyzed side.	18·381	....	Same as Case I.
Do. Sound side...	66·396	0·062	0·808.
Case III. Paralyzed side.	21·842	....	Same as Case I.
Do. Sound side...	52·261	0·031	0·579.

The result of these examinations is very interesting: not a single crystal of cholesterine was found in any of the three specimens of blood from the paralyzed side, while about the normal quantity was found in the blood from the sound side. As the nutrition of other tissues is interfered with in paralysis, it is impossible to say positively, from these observations alone, that cholesterine is produced in the nervous system only. But the nutrition of the nerves is undoubtedly most affected; and these observations, taken in connection with the preceding experiments on animals, point very strongly to such a conclusion.

Our experiments upon animals were so marked and invariable in their results, even when performed under different conditions, that they leave hardly any doubt of the fact that the blood, in passing through the brain, takes up cholesterine. It is more difficult to show, by actual demonstration, that the general system of nerves also gives up cholesterine to the blood; but the fact that the venous blood coming from the extremities contains more cholesterine than the arterial blood, taken in connection with the fact that none of the tissues of the extremities contain cholesterine, except the nerves, renders it more than probable that the nerves, as well as the brain, are the seat of the formation of this principle.

Elimination of Cholesterine by the Liver.—We attempted to demonstrate experimentally the separation of cholesterine from the blood by the liver, in the same way that we determined its passage into the blood circulating through the brain. In the first series of experiments upon this subject, we endeavored to show, in the same animal, the origin of cholesterine in certain parts, and the mechanism of its elimination. In these experiments, which were only approximative, as we had not then succeeded in extracting the cholesterine perfectly pure, we commenced with the arterial blood, examining it as it went to the brain by the carotid, analyzing the substance of the brain, then analyzing the blood as it came from the brain by the internal jugular, examining the blood as it went to the liver by the hepatic artery and portal vein, examining the secretion of the liver, then the blood as it came from the liver by the hepatic vein, examining, also, the blood of the abdominal vena cava. The analyses of the blood from the carotid, internal jugular, and vena cava, have already been referred to in treating of the origin of cholesterine. It will be remembered that there was a large quantity of this substance in the internal jugular, and but a small quantity in the carotid, showing that it was formed in the brain. We now give the conclusion of these observations, which bears upon the separation of cholesterine from the blood:

Experiment I.—Specimens of blood were taken from the hepatic artery, portal vein, and hepatic vein, and a small quantity of bile was taken from the gall-bladder. These specimens were treated in the manner already indicated; viz., evaporated and pulverized, extracted with ether, the ether evaporated and the residue extracted with boiling alcohol, this evaporated, a solution of caustic potash added, and the specimen then subjected to microscopical examination.

Microscopical examination of the extract from the portal vein showed quite a number of crystals of cholesterine. These were observed after the fluid had nearly evaporated.

Microscopical examination of the extract from the hepatic artery, made after the fluid had nearly evaporated, showed a considerable quantity of cholesterine, more than was observed in the preceding specimen. There were also observed a few crystals of stercorine.

The first examination of the extract from the hepatic vein, which was made just before the potash was added, showed a number of fatty masses, with some crystals of stercorine. The solution of potash was then added, and, two days after, another careful examination was made, revealing nothing but fatty globules and granules. The watch-glass was then set aside and was examined eleven days after, when the fluid had entirely evaporated. At this examination, a few crystals of cholesterine were observed for the first time. There were also a number of crystals of margaric and stearic acid.

All the examinations of the extract from the bile showed cholesterine; and the precipitate consisted, indeed, of this substance in a nearly pure state.

Taking these experiments in connection with the first observations upon the carotid and internal jugular, while the one series demonstrates pretty conclusively that cholesterine is formed in the brain, the other shows that it disappears, in a measure, from the blood in its passage through the liver, and is passed into the bile. In other words, it is formed in the nervous tissue and is prevented from accumulating in the blood by its excretion by the liver. This suggests an interesting series of inquiries; and this fact, fully substantiated, would be as important to the pathologist as to the physiologist. But, in order to settle this question, it is necessary to do something more than make an approximative estimate of the quantity of cholesterine removed from the blood by the liver. The quantity thus removed in the passage of the blood through this organ should be estimated, if possible, as closely as the quantity which the blood gains in its passage through the brain. This estimate, however, is more difficult. The operation for obtaining the specimens of blood, in the first place, is much more serious than that for collecting blood from the carotid and internal jugular. It is very difficult to take the unmixed blood from the hepatic vein; and the exposure of the liver, if prolonged, may interfere with its eliminative function, in the same way that exposure of the kidneys arrests, in a few moments, the flow from the ureters. It is probable, however, that the administration of ether does not interfere with the elimination of cholesterine by the liver, as it does, apparently, with its formation in the brain. Anæsthetics, as we know, have a peculiar and special action upon the brain, but they do not appear to interfere with the functions of vegetative life, such as secretion or excretion; and, we may suppose, they would not interfere with the depurative function of the liver. It is fortunate that this is the case, for the operation of taking blood from the abdominal vessels is immensely increased in difficulty by the struggles of an animal that is not under the influence of an anæsthetic.

With the view of settling the question of the disappearance of a portion of the cholesterine of the blood in its passage through the liver, by an accurate quantitative analysis, we repeated the operation for drawing blood from the vessels which go into and emerge from the liver. In the first trial, the blood was drawn so unsatisfactorily, and the operation was so prolonged, that it was not thought worth while to complete the analysis, and the experiment was abandoned. In the following experiment we were more successful.

Experiment II.—A good-sized bitch (pregnant) was brought completely under the influence of ether, the abdomen was laid freely open, and blood was drawn, first from the hepatic vein, and next from the portal vein. The taking of the blood was entirely satisfactory, the operation being done rapidly, and the blood collected without any admixture. A specimen of blood was then taken from the carotid, to represent the blood from the hepatic artery, assuming that the arterial blood is of uniform composition.

The three specimens of blood were then examined in the usual way for cholesterine, with the following results

	Quantity of blood.	Cholesterine.	Cholesterine per 1,000 pts.
	grains.	*grains.*	
Arterial blood.	159·537	0·200	1·257
Portal vein	168·257	0·170	1·009
Hepatic vein	79·848	0·077	0·964
Percentage of loss in arterial blood in its passage through the liver			23·309
Percentage of loss in the blood of the portal vein			4·460

This experiment proves positively, what there was good ground for supposing from Experiment I., that cholesterine is separated from the blood by the liver; and here we may note, in passing, a striking coincidence between the analysis in a previous experiment, in which the blood was studied in its passage through the brain, and the one just mentioned, where the blood was examined after its passage through the liver. The gain of the arterial blood in cholesterine in passing through the brain was 23·307 per cent., and the loss of this substance in passing through the liver is 23·309 per cent. There must be, of course, the same quantity separated by the liver as is produced by the nervous system, it being formed, indeed, only to be separated by this organ, its formation being continuous, and its removal necessarily the same, in order to prevent its accumulation in the circulating fluid. The almost exact coincidence between these two quantities, in specimens taken from different animals, though not at all necessary to prove the fact just mentioned, is still very striking.

It is shown by Experiment II. that the portal blood, as it goes into the liver, contains but a small percentage of cholesterine over the blood of the hepatic vein, while the percentage in the arterial blood is large. The arterial blood is the mixed blood of the entire system; and, as it probably passes through no organ which diminishes its cholesterine before it gets to the liver, it contains a quantity of this substance which must be removed. The portal blood, coming from a limited part of the system, contains less cholesterine, although it gives up a certain quantity. In the circulation in the liver, the portal system largely predominates and is necessary to other important functions of this organ, such as the production of sugar; but, soon after the portal vein enters the liver, its blood becomes mixed with that from the hepatic artery, and from this mixture the cholesterine is separated. It is only necessary that blood, containing a certain quantity of cholesterine, should come in contact with the bile-secreting cells, in order that this substance shall be separated. The fact that it is eliminated by the liver is proven with much less difficulty than that it is formed in the nervous system. In fact, its presence in the bile, and the necessity of its constant removal from the blood, consequent on its constant formation and absorption by this fluid, are almost sufficient in themselves to warrant the conclusion that it is eliminated by the liver. This, however, is put beyond a doubt by the preceding analyses of the blood going to and coming from this organ.

In treating of the composition of the fæces, we have considered so fully the changes which the cholesterine of the bile undergoes in its passage down the intestinal canal, that it is not necessary to refer to this portion of the subject again. We have made but one examination of the quantity of stercorine contained in the daily fecal evacuation, and, assuming that the amount of cholesterine excreted by the liver in twenty-four hours is equal to the amount of stercorine found in the evacuations, the quantity is about ten and a half grains. This corresponds with the estimates of the daily quantity of cholesterine excreted, calculated from its proportion in the bile and the estimated daily amount of bile produced by the liver.

To complete the chain of the evidence leading to the conclusion that cholesterine is an excrementitious principle which is formed in certain of the tissues and eliminated by the liver, it is only necessary to show that it is liable to accumulate in the blood when the eliminating function of the liver is interrupted. It will be remembered that it was only after extirpation of the kidneys, followed by accumulation of urea in the blood, that Prévost and Dumas were able to demonstrate the preëxistence of this principle in the circulating fluid and to indicate the mechanism of its separation from the blood by the kidneys. This mode of study has been applied to certain of the elements of the bile, though without success; for Müller, Kunde, Lehmann, and Moleschott, who extirpated the livers from frogs, looked in the blood only for the biliary salts. We have not been able to repeat these experiments upon frogs and analyze the blood for cholesterine, but we have arrived at very positive results in the study of the blood in diseased conditions of the liver, that are interesting alike to the physiologist and the pathologist.

It has long been recognized that cases of ordinary icterus are not of a grave character, while there are instances in which the jaundice, though less marked as regards coloration of the skin, is a very different condition. Chemists have analyzed the blood, in the hope of explaining this difference by the presence, in the grave cases, of the taurocholate and glycocholate of soda; but their failure to detect these principles leaves the question still uncertain. The real distinction, arguing from purely theoretical considerations, would lie in the proposition that, in cases of simple jaundice, there is merely a resorption from the biliary passages of the coloring matter of the bile, and, in grave cases—which are almost invariably fatal—there is retention of cholesterine in the blood.

We have not been able, on account of the insolubility of cholesterine, to observe the effects of injecting it into the blood-vessels, but we have had an opportunity of making an examination of the blood of a patient in the last stages of cirrhosis of the liver, accompanied with jaundice, and we compared it with an examination of the blood of a patient suffering from simple icterus. Both of these patients had decoloration of the fæces; but in the first the icterus was a grave symptom, accompanying the last stages of disorganization of the liver, while in the latter it was simply dependent on duodenitis, and the prognosis was favorable and verified by the result. As icterus accompanying jaundice is of very infrequent occurrence, we were fortunate in having an opportunity of comparing the two cases.

Without giving in full the details of these cases and the examinations, which are contained in our original memoir on cholesterine, it is sufficient here to state the main results of the examinations of the blood and fæces.

In the case of simple jaundice from duodenitis, in which there was no great disturbance of the system, a specimen of blood, taken from the arm, presented undoubted evidences of the coloring matter of the bile, but the proportion of cholesterine was not increased, being only 0·508 of a part per thousand. The fæces contained a large proportion of saponifiable fat, but no cholesterine or stercorine.

In the case of cirrhosis with jaundice, there were ascites and great general prostration. This patient died a few days after the blood and fæces had been examined, and the liver was found in a condition of cirrhosis, with the liver-cells shrunken, and the gall-bladder contracted. In this case the blood contained 1·850 pt. of cholesterine per thousand, more than double the largest quantity we had ever found in health. The fæces contained a small quantity of stercorine.

Inasmuch as cases frequently present themselves in which there are evidences of cirrhosis of the liver, with little if any constitutional disturbance, while others are attended with grave nervous symptoms, it seemed an interesting question to determine whether it be possible for cholesterine to accumulate in the blood without the ordinary evidence of jaundice. We had an opportunity of examining the blood in two strongly-contrasted cases of cirrhosis, in neither of which was there jaundice.

One of these patients had been tapped repeatedly (about thirty times), but the ascites was the only troublesome symptom, and his general health was pretty good. In this case the proportion of cholesterine in the blood was only 0·246 of a part per thousand, considerably below the quantity that we had found in health.

The other patient had cirrhosis, but he was confined to the bed and was very feeble. The proportion of cholesterine in the blood in this case was 0·922 of a part per thousand, a little above the largest proportion we had found in health.

Like the examinations of the blood in the three cases of paralysis, these pathological observations are not sufficient, in themselves, to establish the function of cholesterine; but, taken in connection with our other experiments, they fully confirm our views with regard to the excretory function of the liver. It is pretty certain that organic disease of the liver, accompanied with grave symptoms generally affecting the nervous system, does not differ in its pathology from cases of simple jaundice in the fact of retention of the biliary salts in the blood; but these grave symptoms, it is more than probable, are due to a deficiency in the elimination of cholesterine—the true excrementitious principle of the bile—and its consequent accumulation in the system. Like the accumulation of urea in structural disease of the kidney, this produces blood-poisoning; and we have characterized this condition by the name Cholesteræmia, a term expressing a pathological condition, but at the same time indicating the physiological relations of cholesterine.

Since the first publication of the preceding observations, numerous experiments have been made upon the relations of cholesterine to nutrition and disassimilation; but most of those observations in which attempts were made to produce toxic effects by injecting cholesterine into the blood have been unsuccessful. In 1873, Koloman Müller (*Ueber Cholesterämie.—Archiv für experimentelle Pathologie und Pharmakologie*, Leipzig, 1873, Bd. i., S. 213, *et seq.*) succeeded in injecting cholesterine without producing any bad effects by mechanical obstruction of the blood-vessels. He made a preparation by rubbing cholesterine with glycerine and mixing the mass with soap and water. He injected into the veins of dogs, 2·16 fluidounces of this solution, containing about 69 grains of cholesterine. In five experiments of this kind, he produced a complete representation of the phenomena of "grave jaundice." Müller's experiments are in exact accordance with our views concerning the physiological and pathological relations of cholesterine. Picot (*Journal de l'anatomie*, Paris, 1872, tome viii., p. 246, *et seq.*) has reported a fatal case of "grave jaundice," in which he determined a great increase in the proportion of cholesterine in the blood, the quantity being 1·804 per 1,000.

In view of all of these facts, the missing link in our own chain of evidence having been supplied by the experiments of Müller, the excrementitious function of the liver, consisting in the separation of cholesterine from the blood and its discharge in the fæces in the form of stercorine, must, we think, be regarded as definitely established.

Production of Sugar in the Liver.

It was formerly supposed that the chief and the only important office of the liver was to produce bile, and all physiological researches into the functions of this organ were then directed to the question of the uses of the biliary secretion; but, in 1848, it was announced by Bernard that he had discovered in the liver a new and important function, and he proceeded to show, by an ingeniously-conceived series of experiments, that the liver is constantly producing sugar of the variety that had long been recognized in the urine of persons suffering from diabetes mellitus. The great physiological and pathological importance of the discovery, attested, as it was, by experiments which seemed to be positively conclusive in their results, excited the most profound scientific interest. During the present century, indeed, there have been few physiological questions that have attracted so much attention; and the observations of Bernard were soon repeated, modified, and extended by experimentalists in different parts of the world. In 1857, Bernard discovered a sugar-forming material in the liver, analogous in its composition and properties to starch; and this seemed to complete the history of glycogenesis.

Shortly after the publication of the glycogenic theory, it was found that other changes were effected in the blood in its passage through the liver; and physiologists then understood, for the first time, how glandular organs might produce secretions and yet not discharge them into excretory ducts. This, indeed, pointed the way to the explanation of the function of the ductless glands. It is perfectly correct to say that the liver secretes sugar; but the secretion, in this instance, is carried away by the blood, and, from this point of view, the liver is to be regarded as a ductless gland. It is evident, therefore, that, even after having studied fully the secretion and the physiological relations of the bile, we have to consider other glandular functions of the liver which are hardly less important.

Evidences of a Glycogenic Function in the Liver.—The proof of the glycogenic function of the liver rests upon the fact, experimentally demonstrated by Bernard, that, in all animals, the blood coming from the liver by the hepatic veins contains sugar, and that the presence of this principle here is not dependent upon the starch or sugar of the food. Bernard assumes to have proven that, in carnivorous animals, never having taken starch or sugar into the alimentary canal except in the milk, there is no sugar in the blood of the portal vein as it passes into the liver; but, under normal conditions, the blood of the hepatic veins always contains sugar. Having examined the blood from various parts of the body and made extracts of all the other tissues and organs, Bernard was unable to find sugar in any other situations than in the liver and the blood coming from the liver. As the blood from the liver is mixed in the vena cava with the blood from the lower extremities, and in the right side of the heart, with the blood from the descending cava, the amount of sugar is proportionately diminished in passing from the liver to the heart. It was found that the sugar generally disappeared in the lungs and did not exist in the blood of the arterial system. Assuming that these statements have been sustained by experimental facts, there can be no doubt that the liver produces or secretes sugar, that this secretion is taken up by the blood, and that the sugar is destroyed in its passage through the lungs.

The question of the production of sugar in the economy has given rise to a great deal of discussion, and the experiments of Bernard have been repeated very extensively. Many physiologists of high authority have been able to verify these observations in every particular; but others have published accounts of experiments which seem to disprove the whole theory.

There can be no doubt of the fact that sugar may, under certain conditions, be produced *de novo* in the organism. Cases of diabetes, in which the discharge of sugar by the urine continues, to a certain extent, when no starch or sugar is taken as food, are conclusive evidence of this proposition. It is a fact equally well established, that the sugar taken as food and resulting from the digestion of starch is consumed in the organism and is never discharged. The fact with regard to diabetes shows, then, that it is not impossible, when no sugar or starch is taken as food, that sugar should be produced in the body; and the failure to find the sugar of the food in the blood or excreta shows that this principle is normally destroyed or consumed in the organism. It only remains, therefore, to determine whether the production of sugar in diabetes be a new pathological process or merely the exaggeration of a physiological function.

We have so often repeated and verified the observations of Bernard, both in experiments made for purposes of investigation and in public demonstrations, that we can entertain no doubt with regard to the glycogenic function of the liver. We have, however, made some late observations which have modified our views concerning the mechanism of glycogenesis; but the fact of the production of sugar in the healthy organism is not affected. Notwithstanding that it seems so easy to verify these experiments, there is, particularly in Great Britain, a pretty wide-spread conviction, that the liver does not produce sugar during life, and that the sugar found by Bernard and others is due to post-mortem action. This view is based chiefly upon the observations of Dr. Pavy, of Guy's Hospital; but it has been adopted by some authorities in Germany and in France. In this state of the question, it will not be sufficient to detail merely the experiments that seem to demonstrate the glycogenic function, but it will be necessary to examine these observations critically and compare them with experiments which lead, apparently, to opposite conclusions; for it is but fair to admit that the observations of Pavy seem to be as accurate, and, at the first blush, as conclusive as those of Bernard.

In the account of the discovery, given by Bernard, it appears that he first sought for the situation in the body where the sugar derived from alimentary substances is destroyed. With this end in view, he fed a dog for seven days with articles containing a large proportion of sugar and starch. On analyzing the blood from the portal system, he found a large proportion of sugar; and he also found it in the blood of the hepatic veins. As a counter-experiment, he fed a dog for seven days exclusively on meat and then looked for sugar in the blood of the hepatic veins; and, to his surprise, he found it in abundance. This experiment he repeated frequently with the greatest care and always with the same result; and he concluded that sugar was formed in the liver and was contained in the blood coming from this organ independently of the diet of the animal. He afterward made extracts of the substance of the liver and of the other tissues, and he found that this organ always contained sugar, while it was not to be detected in any other organ or tissue in the economy. In subsequent experiments, it was demonstrated that the livers of nearly all classes of animals contained sugar, and that it existed also in the human subject. He made observations, also, upon the mechanism of its production, its disappearance in the blood circulating through the lungs, and the various influences which modify the glycogenic function. These points will be considered in their appropriate place; and we shall now proceed, after examining the processes for the determination of sugar, to take up, *seriatim*, the following questions:

1. The absence of sugar from the blood of the portal system in animals that have taken neither starch nor sugar into the alimentary canal.
2. The presence of sugar in the blood as it comes directly from the liver by the hepatic veins, independently of saccharine or amylaceous food.
3. The mechanism of the production of sugar by the liver.

Processes for the Determination of Sugar.—In Bernard's first observations upon the liver, he applied the fermentation-test to a simple decoction of the hepatic substance and obtained unmistakable evidences of sugar. In operating upon perfectly fresh and normal blood, the addition of water and subsequent filtration frequently sufficed to procure a clear solution, to which the ordinary copper-tests could be applied; but the most satisfactory method of making a clear extract was to boil the blood with water and an excess of sulphate of soda. By this means a clear extract can be obtained, containing, it is true, a large quantity of sulphate of soda, but this salt, fortunately, does not interfere with the tests. Later, Bernard decolorized his solutions and extracts by making the liquid into a paste with animal charcoal and filtering. We have long been in the habit of employing both of these methods; but, when we have simply desired to determine the presence or absence of sugar, the process with the sulphate of soda has proved the more convenient. In delicate examinations, however, we have generally used animal charcoal. We have used both methods in decolorizing the decoction of the liver-substance, as well as in operating upon the blood.

In ordinary examinations, Trommer's test is sufficiently delicate; but it is not so sensitive or so convenient as some of the standard test-solutions. We have been in the habit of using, for the determination of sugar in the urine, a modification of Fehling's test, which is also very convenient for examinations of the blood and liver-extract. This may be used as well for quantitative examinations; but, like all of the standard solutions, it presents the inconvenience of undergoing alteration by keeping, so that it is desirable to use it freshly made for each series of examinations. We have succeeded in obviating this difficulty, however, by the following modification in its preparation; and, made in this way, it is probably the most convenient test that can be used in the examination of any of the animal fluids for sugar.

Fehling's Test for Sugar.—The modification in this test consists simply in preparing three separate solutions, which are to be mixed just before using, as follows:

Solution of crystallized sulphate of copper, 94·73 grains in an ounce of distilled water.

Solution of neutral tartrate of potash, 378·91 grains in an ounce of distilled water.

Solution of caustic soda, specific gravity 1·12.

These solutions are to be kept in separate bottles and used as follows:

Take half of a fluidrachm of the copper-solution, add half a fluidrachm of the tartrate of potash, and add the caustic soda, to make three fluidrachms. It is important to measure the copper-solution with accuracy, in quantitative analyses, as the quantity of copper decomposed indicates the amount of sugar.

To apply Fehling's test in ordinary qualitative analyses, heat a small portion of the test-liquid to the boiling-point in a test-tube, and add the suspected fluid, drop by drop. If sugar be present in even a moderate quantity, a dense, yellowish precipitate of the suboxide of copper will be produced after adding a few drops; and, if the liquid be added to about the same volume as the test, and the mixture be again raised to the boiling-point without producing any deposit, it is certain that no sugar is present. The estimation of the quantity of sugar in any liquid depends upon the fact that two hundred grains of the test-liquid is decolorized by exactly one grain of glucose. To apply this test, measure off, in a glass specially graduated for the purpose, two hundred grains of the solution; put this into a flask, with about twice its volume of distilled water, and boil; when boiling, add the suspected solution, little by little, from a burette graduated in grains (raising the mixture to the boiling-point each time and afterward allowing the precipitate to subside), until the blue color is completely discharged; by then reading off the number of grains of the saccharine solution that has been added, the proportion of sugar may be readily calculated. If the solution be suspected to contain a considerable quantity of sugar, the estimate may be more accurately made by diluting it to a known degree, say with nine parts of water, and adding this diluted mixture to the test-liquid.

Examination of the Blood of the Portal System for Sugar.—If starch or sugar be taken into the alimentary canal, it is well known that sugar is always to be found, during absorption, in the blood of the portal system; but, in carnivorous animals, that have been fed entirely upon meat, no sugar can be discovered in the portal blood. The statements of Bernard are very definite upon this point, and he indicates a liability to error when the operation of tying the portal vein has not been skilfully performed, and when blood, containing sugar, is allowed to regurgitate from the substance of the liver. In taking the blood just before it enters the liver, it is necessary to apply a ligature to the vessels as they penetrate at the transverse fissure. This should be done quickly, and the opening into the abdominal cavity should be small. Otherwise, as the vessels have no valves, we are liable to have reflux of blood from the liver. We have frequently performed the experiment, after the method described by Bernard, making a small opening in the linea alba a little below the ensiform cartilage, just large enough to admit the forefinger of the left hand; introducing the finger, and feeling along the concave surface of the liver until we are able to seize the vessels; then passing in an aneurism-needle, and constricting the vessels before the abdomen is widely opened, when a firm ligature is applied. When this step of the operation has been satisfactorily performed, we have never found a trace of sugar in the extract from the blood of the portal system, in animals that have been fed upon nitrogenized matter alone.

There can be no doubt that the blood carried to the liver by the portal vein does not contain sugar, in animals fed solely upon nitrogenized matters. The quantity of blood carried to the liver by the hepatic artery is insignificant; and, although the arterial blood may temporarily contain a trace of sugar, as we shall see farther on, this need not complicate the question under consideration, as the presence of sugar in the blood of the hepatic artery is exceptional, and its proportion, when it exists, is very minute.

Examination of the Blood of the Hepatic Veins for Sugar.—It is upon this question that the whole doctrine of the sugar-producing function of the liver must rest. If it can be proven that the blood, taken from the hepatic veins during life or immediately after death, normally contains sugar, while the blood distributed to the liver contains neither sugar nor any substance that can be immediately converted into sugar, the inevitable conclusion is that the liver is a sugar-producing organ. We shall, consequently, examine this part of the question with the care which its importance demands.

The proposition that the blood from the hepatic veins does not contain sugar during life and health cannot be sustained by actual experiment. Observers may say that the quantity is very slight, but its existence in this situation, independently of the kind of food taken, cannot be denied. Dr. Pavy, who is the originator of the theory that the sugar found in the liver and in the blood coming from the liver is due to a post-mortem change, nowhere states that he has taken the blood from the hepatic veins and failed to find sugar. He says that he has found the blood taken from the right side of the heart by catheterization, in a living animal, "scarcely at all impregnated with saccharine matter," but he does not deny its presence in small quantity. In twelve examinations made by Dr. M'Donnell, of Dublin, traces of sugar were found in five specimens of blood taken from the right auricle by catheterization, in the living animal, and no sugar was detected in seven. It must be remembered, in considering these experiments, that the blood of the right side of the heart is the mixed blood from the entire body; and, assuming that the hepatic blood is constantly saccharine, the quantity in the blood of the right heart would not be very great. In opposition to these experiments, which are only partially negative, we have the following results of examinations of the blood of the hepatic veins and of the right side of the heart, taken as nearly as possible under normal conditions.

To demonstrate the absence of sugar in the portal vein and its constant presence in the hepatic veins in dogs fed exclusively upon meat, Bernard employed the following process: The animal was killed instantly by section of the medulla oblongata. A small opening was then made into the abdomen, just large enough to admit the finger and to enable him to seize the portal vein as it enters at the transverse fissure and to apply a ligature. The abdomen was then freely opened and a ligature was applied to the vena cava just above the renal veins, to shut off the blood from the posterior extremities. The chest was then opened, and a ligature was applied to the vena cava just above the opening of the hepatic veins. Operating in this way, blood may be taken from the portal system before it enters the liver, and from the hepatic veins as it passes out. In the blood from the portal system no sugar is to be found, but its presence is unmistakable in the blood from the hepatic veins. To avoid disturbing the circulation in the liver, and in order to collect from the hepatic veins as large a quantity of blood as possible, Bernard modified the experiment, in some instances, by introducing into the vena cava in the abdomen a double sound, the extremity of which is provided with a bulb of India-rubber. This was pushed into the vein above the diaphragm; and, by inflating the bulb, the vein was obstructed above the liver, and the blood could be collected through one of the canulæ, as it came directly from the hepatic vessels. Bernard never failed to determine the presence of sugar in these specimens of blood, employing a number of different processes, including the fermentation-test and even collecting the alcohol. To complete the proof of the existence of sugar in the blood coming from the liver, Bernard demonstrated its presence in blood taken from the right auricle in a living animal, which can be readily done by introducing a catheter into the right side of the heart through an opening in the external jugular vein. He also showed that, during digestion, the whole mass of blood contained sugar, but that the quantity was greater in the right side of the heart than in the arterial system.

It is unnecessary to cite all the authorities that have confirmed the observations of Bernard. Shortly after these experiments were published, Lehmann, Frerichs, and many others verified their accuracy. Bernard gives in full the experiments of Poggiale and of Leconte, the results of which were identical with his own. He gives, also, in one of his later works, the proportions of sugar in the blood of the hepatic veins, obtained by Lehmann, Schmidt, Poggiale, and Leconte, no sugar being found in the blood of the portal system. We have ourselves made a number of experiments with a view of harmonizing, if possible, the discordant observations of Bernard and Pavy, and have examined the blood from the hepatic veins for sugar, taking the specimens under what seemed to be strictly physiological conditions. In one of these published experiments, blood was taken from the hepatic veins of a large dog, fully-grown and fed regularly every day but not in digestion at the time of the experiment, and the operation lasted only seventy seconds. No anæsthetic was employed. The extract of this specimen of blood, treated with Fehling's test-liquid, presented a well-marked deposit of the oxide of copper, revealing unequivocally the presence of a small quantity of sugar.[1] This has been the invariable result in numerous experiments and class-demonstrations made since 1858; and, since the experiments just referred to were published, we have verified the observation with regard to the hepatic blood, keeping the animal perfectly quiet before the operation, avoiding the administration of an anæsthetic, and taking the blood so rap-

FIG. 137.—*Catheter for the right side of the heart.* (Bernard.)

E, extremity of the tube; R, stop-cock; *e*, extremity to be introduced into the right auricle.

The tube is introduced through a small opening into the external jugular vein, the concavity of the tube turned toward the sternum, and the stop-cock closed. When the tube reaches the heart, we feel the pulsations, and the jet of blood, when the stop-cock is opened, is intermittent.

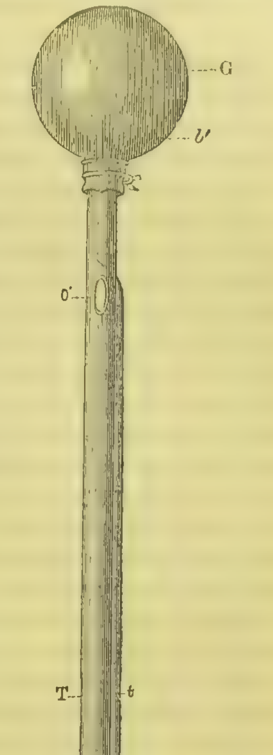


FIG. 138.—*Double sound, used for collecting blood from the hepatic veins.* (Bernard.)

o, *t*, *o'*, tube, with a stop-cock (*r*), used to inflate the rubber bulb (G, *b'*); O, T, tube, with an opening (*o'*), which receives the blood from the hepatic veins, and is provided with a stop-cock (R).

[1] FLINT, JR., *Experiments undertaken for the Purpose of reconciling some of the Discordant Observations upon the Glycogenic Function of the Liver.—New York Medical Journal*, 1869, vol. viii., p. 381. These experi-

idly that no sugar could be formed by the liver post mortem. These experiments leave no doubt of the fact that, during life and in health, the blood, as it passes through the liver and is discharged by the hepatic veins into the vena cava, contains sugar, which is formed by the liver, independently of the sugar and starch taken as food.

Does the Liver contain Sugar normally during Life?—This is the only question upon which the results of reliable experiments have been entirely opposite. Bernard made the greater part of his observations by analyzing the substance of the liver; and he arrived at most of his conclusions with regard to the variations in the glycogenic function, from estimates of the proportion of sugar in the liver under different conditions. For many years we have been in the habit of repeating these experiments, with like results, and we have never failed to find sugar under normal conditions of the system. We were formerly in the habit of making the demonstrations of the formation of sugar in the liver upon animals that had been etherized; and then we always obtained a brilliant precipitate from the clear extract of the substance of the liver boiled with the test-liquid. The experiment was performed in this way before we had acquired sufficient dexterity to seize the portal vein readily and to go through with the necessary manipulations with rapidity. We subsequently made the operation by first suddenly breaking up the medulla oblongata, then making a small incision into the abdominal cavity, seizing the portal vein instantly, and following out the remaining steps of the experiment without delay. In this way, although sugar was always found in the blood of the hepatic veins, we frequently failed to obtain a distinct reaction in the extract of the liver; and it appeared, indeed, that the more accurately and rapidly the operation was performed, the more difficult was it to detect sugar in the hepatic substance. It seems probable, in reflecting upon these facts, that, inasmuch as no one has assumed that the actual quantity of sugar produced by the liver is very considerable, and as a large quantity of blood (in which the sugar is very soluble) is constantly passing through the liver, precisely as we pass water through its vessels to remove the sugar, the sugar might be washed out by the blood as fast as it is formed; and that really the liver might never contain sugar in its substance, as a physiological condition, although it is constantly engaged in its production. We know that the characteristic elements of the various secretions proper are produced in the substance of the glands and are washed out at the proper time by liquid derived from the blood, which circulates in their substance during their functional activity in very much greater quantity than during the intervals of secretion. Now, the liver-sugar may certainly be regarded as an element of secretion; and, possibly, it may be completely washed out of the liver, as fast as it is formed, by the current of blood, the hepatic vein, in this regard, serving as an excretory duct. To put this hypothesis to the test of experiment, it was necessary to obtain and analyze a specimen of the liver in a condition as near as possible to that under which it exists in the living organism; and, in carrying out this idea, we instituted the following experiments:

Experiment I.—A medium-sized dog, full-grown, in good condition, and not in digestion, was held upon the operating-table by two assistants, and the abdomen was widely opened by a single sweep of the knife. A portion of the liver, weighing about two ounces, was then excised and immediately cut into small pieces, which were allowed to fall into boiling water. The time from the first incision until the liver was in the boiling water was twenty-eight seconds. An excess of crystallized sulphate of soda was then added, and the mixture was boiled for about five minutes. It was then thrown upon a filter, and the clear fluid that passed through was tested for sugar by Trommer's test. The reaction was doubtful and afforded no marked evidence of sugar.

Experiment II.—A medium-sized dog, in the same condition as the animal in the first experiment, was held upon the table, and a portion of the liver was excised, as above

ments are the first on record, made with the view above indicated. The experiments by Dr. Lusk and by Dr. Dalton were made later, with the view of confirming our original observations.

described. The whole operation occupied twenty-two seconds. Only ten seconds elapsed from the time the portion of the liver was cut off until it was in the boiling water. It was boiled for about fifteen minutes, made into a paste with animal charcoal, and thrown upon a filter. The clear fluid that passed through was tested for sugar by Trommer's test. There was no marked evidence of sugar.

Experiment III.—A large dog, full-grown and fed regularly every day, but not in digestion at the time of the experiment, was held firmly upon the table. This dog had been in the laboratory about a week and was in a perfectly normal condition. The abdominal cavity was opened, and a piece of the liver was cut off and thrown into boiling water, the time occupied in the process being ten seconds. Before the liver was cut up into the boiling water, the blood was rinsed off in cold water. The liver was boiled for about seventeen minutes, mixed with animal charcoal, and the whole was thrown upon a filter.

Immediately after cutting off a portion of the liver and throwing it into boiling water, the medulla oblongata was broken up, a ligature was applied to the ascending vena cava just above the renal veins, the chest was opened, and a ligature was applied to the vena cava just above the opening of the hepatic veins. A specimen of blood was then taken from the hepatic veins. This portion of the operation occupied not more than one minute. A little water was added to the blood, which was boiled briskly, mixed with animal charcoal, and thrown upon a filter. The liquid that passed through from both specimens was perfectly clear.

While the filtration was going on, Fehling's test-liquid was made up, so as to be perfectly fresh. The two liquids were then carefully tested for sugar. The extract of the liver presented not the slightest trace of sugar. The extract from the blood of the hepatic veins presented a well-marked deposit of the oxide of copper, revealing unequivocally the presence of a small quantity of sugar.

Experiment IV.—This experiment was made upon a medium-sized dog, in full digestion of meat. The medulla oblongata was broken up; the portal vein was tied through a small opening in the abdomen; and the abdomen was then widely opened, and a portion of the liver excised, rapidly rinsed, and cut up into boiling water. The length of time that elapsed between breaking up the medulla and cutting up the specimen of liver into the boiling water was one minute.

The vena cava was then tied above the renal veins, the chest opened, and the cava again tied above the hepatic veins. Blood was then taken from the hepatic veins, about an equal bulk of water was added, with an excess of the crystallized sulphate of soda, and the mixture was boiled. A portion of the portal blood and the decoction of the liver were then treated in the same way, and the three specimens were filtered.

The clear extracts were then tested with Fehling's liquid, with the following result:

There was no sugar in the portal blood.

There was no sugar in the extract of the liver.

There was a marked reaction in the extract of the blood from the hepatic veins, the precipitate rendering the whole solution bright yellow and entirely opaque.

This experiment was made in the presence of the class at the Bellevue Hospital Medical College, January 4, 1869.

The importance of the question under consideration and its present unsettled condition are, we hope, sufficient to justify the introduction of the details of the preceding experiments. They were undertaken with the view of harmonizing, if possible, the facts brought forward by different experimentalists.

It is difficult to imagine how any observer, so well known and accurate as Dr. Pavy, could assert positively, as the result of personal examination, that the liver does not contain sugar when examined immediately after its removal from the living body, when Bernard and so many others have demonstrated its presence in this organ in large quantity. Yet, such was the result of all the experiments of Pavy, and the same conclusion was arrived at by M'Donnell, and afterward by Meissner and Jaeger, and by Schiff. The ingenious experiment of Bernard, showing that sugar is formed in a liver removed from the body and washed sugar-free by a stream of water passed through its vessels, demonstrated the possibility of the production of sugar post mortem, so strongly claimed by Pavy as the only condition under which it is ever formed; still, it does not seem possible to deny the sugar-producing function of the liver, in view of the conclusive experimental proof of the constant presence of glucose in the blood of the hepatic veins.

From our own experiments, we have come to the conclusion that Dr. Pavy and those who adopt his views cannot consistently deny that sugar is constantly formed in the liver and discharged into the blood of the hepatic veins; nor can Bernard and his followers ignore the fact that the liver does not contain sugar during life; although, as has been shown by Pavy, and more specifically by M'Donnell, sugar appears in the liver in great abundance soon after death.

In the experiments that we have just detailed, which are simply typical examples of numerous unrecorded observations, we attempted to verify the observations of Pavy without losing sight of the facts observed by Bernard, and to verify the experiments of Bernard in the face of the apparently contradictory statements of Pavy. When an animal is in perfect health, has been kept quiet before the experiment, and a piece of the liver is taken from him by two sweeps of the knife, the blood rinsed from it and the tissue cut up into water already boiling, the whole operation occupying only ten seconds (as was the case in Experiment III.), the liver is as nearly as possible in the condition in which it exists in the living organism. As this was done repeatedly in animals during digestion and in the intervals of digestion, and an extract was thoroughly made without finding any sugar, we regarded the experiments of Pavy as entirely confirmed and the fact demonstrated that the liver does not contain sugar during life. On the other hand, when we made the experiment upon the liver as above described, and, in addition, took specimens of the portal blood and the blood from the hepatic veins, under strictly physiological conditions (as was done in Experiment IV.), and found no sugar in the portal blood or in the substance of the liver, but an abundance in the blood of the hepatic veins, it was impossible to avoid the conclusion that the sugar was formed in the liver and was washed out in the blood as it passed through.

In treating of the mechanism of the formation of sugar in the liver, we shall describe more fully the glycogenic matter; but, taking into consideration the demonstration of the presence of sugar in the blood of the hepatic veins by Bernard; his discovery of the post-mortem production of sugar in a liver washed sugar-free, probably from a substance remaining in the liver and capable of being transformed into sugar; the negative results of the examinations of the liver for sugar by Pavy; and, adding to this our own experiments upon all of these points, we are justified in adopting the following conclusions:

1. A substance exists in the healthy liver, which is capable of being converted into sugar; and, inasmuch as this is formed into sugar during life, the sugar being washed away by the blood passing through the liver, it is perfectly proper to call it glycogenic, or sugar-forming matter.

2. The liver has a glycogenic function, which consists in the constant formation of sugar out of the glycogenic matter, this being carried away by the blood of the hepatic veins, which always contains sugar in a certain proportion. This production of sugar takes place in the carnivora, as well as in those animals that take sugar and starch as food; and it is, essentially, independent of the kind of food taken.

3. During life, the liver contains the glycogenic matter only and no sugar, because the great mass of blood which is constantly passing through this organ washes out the sugar as fast as it is formed; but, after death or when the circulation is interfered with, the transformation of glycogenic matter into sugar goes on; the sugar is not removed under these conditions, and can then be detected in the substance of the liver.

Characters of the Liver-Sugar.—Very little is to be said regarding the chemical peculiarities of liver-sugar. It resembles glucose, or the sugar resulting from the digestion of starch, in its composition. This sugar, like glucose, responds promptly to all of the copper-tests, and it undergoes transformation into melassic acid on being boiled with an alkali. One of its most marked peculiarities is that it ferments more readily than any other variety of sugar; and another is that it is destroyed in the economy with extraordinary facility. This fact has been illustrated by the following ingenious experiment: Bernard injected under the skin of a rabbit a little more than seven grains of cane-sugar dissolved in about an ounce of water, and he found sugar in the urine. Under the same conditions, he found he could inject seven grains of milk-sugar, fourteen and a half grains of glucose, twenty-one and a half grains of diabetic sugar, and nearly thirty grains of liver-sugar, without finding any sugar in the urine; showing that the liver-sugar is consumed in the organism more rapidly and completely than any other saccharine principle.

Mechanism of the Production of Sugar in the Liver.—When Bernard first described the glycogenic function of the liver, he thought that the sugar was produced from nitrogenized principles, in some manner which he did not attempt to explain. Subsequent discoveries, however, have led to conclusions entirely different.

In 1855, Bernard first published an account of his remarkable experiment showing the post-mortem production of sugar. After washing out the liver with water passed through the vessels until it no longer contained a vestige of sugar, it was allowed to remain at about the temperature of the body for a few hours and was then found to contain sugar in abundance. This experiment we have already referred to, and it is one that we have frequently verified. Bernard explained the phenomenon by the supposition, subsequently shown to be correct, that the liver contains a peculiar principle, slightly soluble in water and capable of transformation into sugar.

Glycogenic Matter.—In its composition, reactions, and particularly in the facility with which it undergoes transformation into sugar, glycogenic matter bears a very close resemblance to starch. It is described by Pavy under the name of amyloid matter, a name which is applied to it, also, by Rouget. It is insoluble in water, and, by virtue of this property, it may be extracted from the liver after the sugar has been washed out. The following is the method for its extraction proposed by Bernard:

The liver of a small and young animal, like the rabbit, in full digestion, presents the most favorable conditions for the extraction of the glycogenic matter. The liver is taken from the animal immediately after it is killed, is cut into thin slices, and thrown into boiling water. When the tissue is hardened, it is removed and ground into a pulp in a mortar. It is then boiled a second time in the water of the first decoction, strained through a cloth, and the opaline liquid which passes through is made into a thin paste with animal charcoal. The paste is then put into a displacement-apparatus, the end of which is loosely filled with shreds of moistened cotton. By successive washings, the paste is exhausted of its glycogenic matter, leaving behind the albuminoid and coloring matters. The whitish liquid, as it flows, is received into a vessel of absolute alcohol, when, as each drop falls, the glycogenic matter is precipitated in white flakes. This is filtered and dried rapidly in a current of air. If the alcohol be not allowed to become too dilute, the matter when dried is white and easily pulverized. The substance thus obtained may be held in suspension in water, giving to the liquid a strongly opaline appearance. It is neutral, without odor or taste, and presents nothing characteristic under the microscope. It reacts strongly with iodine, which produces a dark-violet or chestnut-brown color, but rarely a well-marked blue. It presents none of the reactions of sugar and is entirely insoluble in alcohol. It is changed into sugar by boiling for a long time with dilute acids, and this conversion is rapidly effected by the saliva, the pancreatic juice, and a peculiar ferment found in the substance of the liver. Prepared in the way above indicated, and pulverized, it may be preserved for an indefinite period.

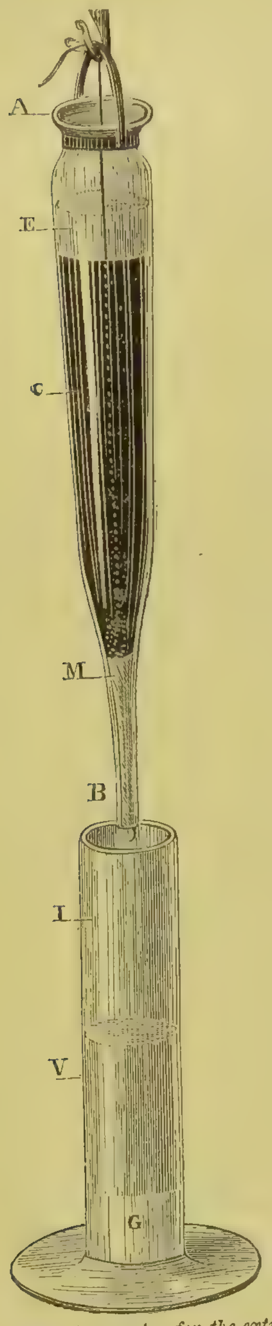


Fig. 139.—*Apparatus for the extraction of glycogenic matter.* (Bernard.)

A B, displacement apparatus in which the filtration takes place; C, animal charcoal mixed with the decoction of the liver; E, glycogenic solution; M, lamp-wicking, attached to a thread, passing through the carbon and coming out at the upper part of the apparatus; I, precipitating-glass; G, glycogenic matter precipitated; V, alcohol.

The peculiar reaction of the glycogenic matter with iodine has led to its recognition in the substance of the liver-cells and in some other situations. Schiff found in the liver-cells minute granulations, which presented the peculiar color on the addition of iodine, characteristic of glycogenic matter. Bernard, a few years after his discovery of this principle in the liver, recognized it in cells attached to the placenta. He believes that these cells produce sugar during the early period of fœtal life, before the liver takes on this function, and that they disappear during the later months, as the liver becomes fully developed.

Since the discovery of the glycogenic function of the liver, anatomists have found amyloid corpuscles in various of the tissues of the body. We do not propose, however, to discuss this question in all its bearings, but only to consider the known relations of the amyloid substances found in the body to the formation of sugar.

In the first place, there can be no doubt of the fact, that the liver of a carnivorous animal that has been fed exclusively on meat contains an amyloid substance readily convertible into sugar. The question of the existence of the same amyloid matter in other tissues and organs is only pertinent in so far as it bears upon the production of sugar or upon the formation of the glycogenic matter in the liver. In no tissue or organ in the adult has it been demonstrated that there is any formation of sugar, except the ordinary transformation of starch into sugar in the process of digestion.

If the liver taken from an animal recently killed be simply kept at about the temperature of the body, after it has been drained of blood or even after it has been washed through the vessels, sugar will be rapidly formed in its substance. This must be due to some ferment remaining in the tissue; and Bernard has, indeed, been able to isolate a principle which exerts this influence in a marked degree. If an opaline decoction of the liver be allowed to stand until it has become entirely clear, showing that all the glycogenic matter has been transformed into sugar, and alcohol be added to the liquid, the hepatic ferment will be precipitated. This may be redissolved in water, and it effects the transformation of starch into sugar with great rapidity. From these facts, it is pretty conclusively shown that the following is the mechanism of the production of sugar in the liver:

The liver first produces a peculiar principle (analogous to starch in its composition and in many of its properties, though it contains two atoms more of water) out of which the sugar is to be formed. The name glycogenic matter may properly be applied to this substance. It is, as far as is known, produced in all classes of animals, carnivora and herbivora; and, although its quantity may be modified by the kind of food, its formation is essentially independent of the alimentary principles absorbed.

The glycogenic matter is not taken up by the blood as it passes through the liver, but is gradually transformed, in the substance of the liver, into sugar, which is washed out of the organ as fast as it is produced. Thus the blood of the hepatic veins always contains sugar, although sugar is not contained in the substance of the liver during life.

Variations in the Glycogenic Function.

In following out the relations of the glycogenic process to the various animal functions, Bernard studied very closely its variations at different periods of life, with digestion, the influence of the nervous system, and other modifying conditions. He made some of his observations by examining the blood in living animals, and others, by estimating the proportion of sugar in the liver. The latter method is to be considered, with an appreciation of the fact that the liver does not normally contain sugar during life; but it represents, to a certain extent, the activity of the glycogenic function. Still, the facts arrived at in this way must be taken with a certain degree of caution.

Glycogenesis in the Fœtus.—In the early months of fœtal life, many of the tissues and fluids of the body were found by Bernard to be strongly saccharine; but at this time no sugar is to be found in the liver. Taking the observations upon fœtal calves as a criterion, sugar does not appear in the liver until toward the fourth or fifth month of intra-uterine life. Before this period, however, epithelial cells filled with glycogenic matter are found in the placenta, and these produce sugar until the liver takes on its functions. As the result of numerous observations by Bernard upon fœtal calves, this function of the placenta appears very early in fœtal life, and, at the third or fourth month, it has attained its maximum. At about this time, when glycogenic matter begins to appear in the liver, the glycogenic organs of the placenta become atrophied, and they disappear some time before birth.

Influence of Digestion and of Different Kinds of Food.—Activity of the digestive organs has a marked influence upon the production of sugar in the liver. In a fasting animal, sugar is always found in the blood of the hepatic veins and in the vessels between the liver and the heart, but it never passes the lungs and does not exist in the arterial system. During digestion, however, even when the diet is entirely nitrogenized, the production of sugar is so much increased that a small quantity frequently escapes decomposition in the lungs and passes into the arterial blood. Under these conditions, the quantity in the arterial blood is sometimes so large that a trace may appear in the urine, as a temporary and exceptional, but not an abnormal condition. This physiological fact is well illustrated in certain cases of diabetes. There are instances, indeed, in which the sugar appears in the urine only during digestion; and, in almost all cases, the quantity of sugar eliminated is largely increased after eating.

The influence of the kind of food upon the glycogenic function is a question of great pathological as well as physiological importance. It is well known to pathologists that certain cases of diabetes are relieved when the patient is confined strictly to a diet containing neither saccharine nor amylaceous principles, and that, almost always, the quantity of sugar discharged is very much diminished by such a course of treatment; but there are instances in which the discharge of sugar continues, in spite of the most carefully-regulated diet. Bernard does not recognize fully the influence of different kinds of food upon glycogenesis, and his experiments on this point are wanting in accuracy, from the fact that the proportion of sugar in the liver is given, without indicating at what period after death the examinations were made. In the observations upon this point by Pavy, the examinations of the liver were made immediately after death, and the proportion of glycogenic matter—not sugar—was estimated. His results are, consequently, much more reliable and satisfactory. In a number of analyses of the livers of dogs confined to different articles of diet, Pavy found a little over seven per cent. of glycogenic matter, upon a diet of animal food; over seventeen per cent., upon a diet of vegetable food; and fourteen and a half per cent., upon a diet of animal food and sugar. These results have been confirmed by M'Donnell, who, in addition, found that hardly a trace of amyloid substance could be detected in the liver upon a diet of fat, and none whatever upon a diet of gelatine. Bernard had already observed that the amount of sugar produced by the liver upon a diet of fat was the same as during total abstinence from food. These facts are entirely in accordance with observations upon the effects of different kinds of food in diabetes, and they have an important bearing upon the dietetic measures to be employed in this disease.

The effect of entire deprivation of food is to arrest the production of sugar in the liver, three or four days before death. This arrest of the glycogenic function has generally been observed in cases of disease, except when death has occurred suddenly.

Influence of the Nervous System, etc.—Bernard has studied the influence of the nervous system upon the production of sugar more satisfactorily than any other of the variations of the glycogenic function, for the reason that he has noted these modifications by determining the sugar in the blood and in the urine. Some of the points with regard to the nervous system we shall consider again, and it is sufficient, in this connection, to mention the main results of some of the most striking of the experiments upon this subject.

Fig. 140.—*Instrument for puncturing the floor of the fourth ventricle.* (Bernard.)

The most remarkable experiment upon the influence of the nervous system on the liver is the one in which artificial diabetes is produced by irritation of the floor of the fourth ventricle. This operation is not difficult, and it is one that we have often repeated. The instrument used is a delicate stilet, with a flat, cutting extremity, and a small, projecting point about $\frac{1}{25}$ of an inch long. In performing the operation upon a rabbit, the head of the animal is firmly held in the left hand, and the skull is penetrated in the median line, just behind the superior occipital protuberance. This can easily be done by a few lateral movements of the instrument. Once within the cranium, the instrument is passed obliquely downward and forward, so as to cross an imaginary line drawn between the two auditory canals, until its point reaches the basilar process of the occipital bone. The point then penetrates the medulla oblongata, between the roots of the auditory nerves and the pneumogastrics, and, by its projection, serves to protect the nervous centre from more serious injury from the cutting edge. The instrument is then carefully withdrawn, and the operation is completed. This experiment is almost painless, and it is not desirable to administer an anæsthetic, as this, in itself, would disturb the glycogenic process. The urine may be drawn before the operation, by pressing the lower part of the abdomen, taking care not to allow the bladder to pass up above the point of pressure, and it will be found turbid, alkaline, and without sugar. In one or two hours after the operation, the urine will have become clear and acid, and it will react readily with any of the copper-tests. When this operation is performed without injuring the adjacent organs, the presence of sugar in the urine is only temporary, and the next day the secretion will have returned to its normal condition. It is best, in performing this experiment, to operate upon an animal in full digestion, when the production of sugar is at its maximum. The production of diabetes in this way, in animals, is exceedingly interesting in its relations to certain cases of the disease in the human subject, in which the affection is traumatic and directly attributable to injury near the medulla. Its mechanism is difficult to explain. The irritation is not propagated through the pneumogastric nerves, for the experiment succeeds after both of these nerves have been divided; but the influence of the pneumogastrics upon glycogenesis is curious and interesting. If both of these nerves be divided in the neck, in a few hours or days, depending upon the length of time that the animal survives the operation, no sugar is to be found in the liver, and there is reason to believe that the glycogenic function has been arrested. After division of the nerves in this situation, galvanization of their peripheral ends does not affect the production of sugar; but, by galvanization of the central ends, an impression is conveyed to the nervous centre, which is reflected to the liver and produces a hypersecretion of sugar. These questions will be referred to again, in connection with the physiology of the nervous system.

FIG. 141.—*Section of the head of a rabbit, showing the operation of puncturing the floor of the fourth ventricle.* (Bernard.)

a, cerebellum; *b*, origin of the seventh pair of nerves; *c*, spinal cord; *d*, origin of the pneumogastric; *e*, opening of entrance of the instrument into the cranial cavity; *f*, instrument; *g*, fifth pair of nerves; *h*, auditory canal; *i*, extremity of the instrument upon the spinal cord after having penetrated the cerebellum; *k*, occipital venous sinus; *l*, tubercula quadrigemina; *m*, cerebrum; *n*, section of the atlas.

With regard to the influence of the sympathetic system upon the glycogenic function, there have been few if any experiments which lead to conclusions of any great value.

It has been observed that the inhalation of anæsthetics and irritating vapors produces temporary diabetes; and this has been attributed to an irritation conveyed by the pneumogastrics to the nerve-centre, and reflected, in the form of a stimulus, to the liver. It is for this reason that we should avoid the administration of anæsthetics in all accurate experiments on the glycogenic function.

Destination of Sugar.—Although sugar is constantly produced by the liver and taken up by the circulation, it is exceptional to find it in the blood after it has passed through the lungs. It is difficult to ascertain the precise mode of its destruction in the lungs, and, indeed, the nutritive function of sugar in the economy is not thoroughly understood. All that we can say of the destination of liver-sugar is, that it probably has the same office in nutrition as the sugar taken as food and that resulting from the digestion of amylaceous matters. The facts bearing upon this question will be reviewed under the head of nutrition.

Alleged Production of Fat by the Liver.—It is stated by Bernard that, in animals fed largely with saccharine and amylaceous principles, the blood of the hepatic veins contains an emulsive matter, which seems to be fat combined with a proteine substance. In support of the opinion that fat is thus produced in the liver, he brings forward the well-known fact, that a diet of starch and sugar is particularly favorable to the development of adipose tissue. But the examinations of the matter supposed to be fatty have not been sufficiently minute to lead to any positive conclusions with regard to its character or composition. While there can be no doubt of the formation of fat in the organism independently of the fat taken as food, there is not sufficient ground for regarding the liver as one of the organs specially concerned in its production.

Changes in the Albuminoid and the Corpuscular Elements of the Blood in passing through the Liver.—In verifying the observations of Bernard upon the presence of sugar in the blood of the hepatic veins, Lehmann was led to observe other differences in the composition of the blood from these vessels, as compared with the portal blood and the blood of the arterial system. One of the most important of these was the absence of coagulating principles. While the portal blood coagulates strongly, like blood from any other part of the body, the blood of the hepatic veins does not coagulate, and "the fibrin is either entirely absent, or is present in mere traces."

Some very curious observations were also made by Lehmann upon the blood-corpuscles in the hepatic vessels. He estimated that the proportion of white corpuscles in the blood of the hepatic veins was at least fivefold the proportion in the portal blood. He also noted certain differences in the appearance of the red corpuscles, which he explained by the supposition that the liver was the seat of development of these elements, which were formed from the white corpuscles, and that the blood of the hepatic veins contained a greater number of "newly-formed or rejuvenescent blood-corpuscles."

It is not our purpose, in this connection, to discuss the development of the corpuscular elements of the blood; but it is interesting to note the above-mentioned changes in the blood as it passes through the liver. The physiological significance of the destruction of albuminoids is not understood, although the fact is undoubted.

CHAPTER XIV.

THE DUCTLESS GLANDS

Probable office of the ductless glands—Anatomy of the spleen—Fibrous structure of the spleen (trabeculæ)—Malpighian bodies—Spleen-pulp—Vessels and nerves of the spleen—Some points in the chemical constitution of the spleen—State of our knowledge concerning the functions of the spleen—Variations in the volume of the spleen—Extirpation of the spleen—Anatomy of the suprarenal capsules—Cortical substance—Medullary substance—Vessels and nerves—Chemical reactions of the suprarenal capsules—State of our knowledge concerning the functions of the suprarenal capsules—Extirpation of the suprarenal capsules—Addison's disease—Anatomy of the thyroid gland—State of our knowledge concerning the functions of the thyroid gland—Anatomy of the thymus—Pituitary body and pineal gland.

Certain organs in the body, with a structure resembling, in some regards, the true glands, but without excretory ducts, have long been the subject of physiological speculation; and the most extravagant notions concerning their functions have prevailed in the early history of the science. The discovery of those functions of the liver which consist in modifications in the composition of the blood passing through its substance dimly foreshadowed the probable office of the ductless glands; for, as far as the production of sugar is concerned, the liver belongs to this class. Indeed, the supposition that the ductless glands effect some change in the blood is now regarded by physiologists as the most reasonable of the many theories that have been entertained concerning their office in the economy. Under this idea, these organs have been called blood-glands or vascular glands; but, inasmuch as the supposition that these parts effect changes in the blood or lymph is merely to supply the want of any definite idea of their function and rests mainly upon analogy with certain of the functions of the liver, we shall retain the name ductless glands, as indicating the most striking of their anatomical peculiarities.

As far as presenting any definite and important physiological information is concerned, we might terminate here the history of the ductless glands. It is true that the largest of them, the spleen, was extensively experimented upon by the earlier physiologists; but, in point of fact, investigations have done little more than exhibit a want of knowledge of the functions of these remarkable organs; and the literature of the subject is mainly a collection of speculations and fruitless experiments. There are, however, some interesting experimental facts with relation to the spleen and the suprarenal capsules, although they are not very instructive, except that they indicate the extremely narrow limits of our positive knowledge. These few facts, with a sketch of the anatomy of the parts, will embrace all that we shall have to say concerning the ductless glands. Under this head are classed, the spleen, the suprarenal capsules, the thyroid gland, the thymus, and sometimes the pituitary body and the pineal gland. These parts have certain anatomical points in common with each other, but, on account of our want of knowledge of their functions, it is difficult to distinguish, as we have done in other organs, their physiological anatomy.

Anatomy of the Spleen.

The spleen is situated in the left hypochondriac region, next the cardiac extremity of the stomach. Its color is of a dark bluish-red, and its consistence is rather soft and friable. It is shaped somewhat like the tongue of a dog, presenting above, a rather thickened extremity, which is in relation with the diaphragm, and below, a pointed extremity, in relation with the transverse colon. Its external surface is convex, and its internal surface, concave, presenting a vertical fissure, the hilum, which gives passage to the vessels and nerves. It is connected with the stomach by the gastro-splenic omentum and is still farther fixed by a fold of the peritoneum passing to the diaphragm. It is about five inches in length, three or four inches in breadth, and a little more than an inch in thickness. Its weight is between six and seven ounces. In the adult it attains its maximum of development, and it diminishes slightly in size and weight in old age. In early life it bears about the same relation to the weight of the body as in the adult.

The external coat of the spleen is the peritoneum, which is very closely adherent to the subjacent fibrous structure. The proper coat is dense and resisting; but, in the human subject, it is quite thin and somewhat translucent. It is composed of inelastic fibrous tissue, mixed with numerous small fibres of elastic tissue and a few unstriped muscular fibres.

At the hilum, the fibrous coat penetrates the substance of the spleen in the form of sheaths for the vessels and nerves; an arrangement analogous to the fibrous sheath of the analogous structures in the liver. The number of the sheaths in the spleen is equal to the number of arteries that penetrate the organ. This membrane is sometimes called the capsule of Malpighi. The fibrous sheaths are closely adherent to the surrounding substance, but they are united to the vessels by a loose fibrous net-work. They follow the vessels in their ramifications to the smallest branches and are lost in the spleen-pulp. Between the sheath and the outer coat, are numerous bands, or trabeculæ, presenting the same structure as the fibrous coat. The presence of elastic fibres in these structures can be easily demonstrated, and this kind of tissue is very abundant in the herbivora. In the carnivora the muscular tissue is particularly abundant and can be readily demonstrated; but in man this is not so easy, and the fibres are less numerous, some anatomists denying the existence of any muscular structure. These peculiarities in the fibrous structure are important in their relation to certain physiological changes in the size of the spleen. Its contractility may be easily demonstrated in the dog by the application of a galvanic current to the nerves as they enter at the hilum. This is followed by a prompt and energetic contraction of the organ. Contractions may be produced, though they are much more feeble, by applying the current directly to the spleen.

The substance of the spleen is soft and friable; and a portion of it, the spleen-pulp, may be easily pressed out, or even washed away by a current of water. Aside from the vessels and nerves, it presents for study: 1. An arrangement of fibrous bands, or trabeculæ, by which it is divided into innumerable communicating cellular interspaces. 2. Closed vesicles (Malpighian bodies), attached to the walls of the blood-vessels. 3. A soft, reddish substance, containing numerous cells and free nuclei, called the spleen-pulp.

Fibrous Structure of the Spleen (Trabeculæ).—From the internal face of the investing membrane of the spleen and from the fibrous sheath of the vessels (capsule of Malpighi), are numerous bands, or trabeculæ, which, by their interlacement, divide the substance of the organ into irregularly-shaped, communicating cavities. These bands are from $\frac{1}{25}$ to $\frac{1}{15}$ of an inch broad, and are composed, like the proper coat, of ordinary fibrous tissue with elastic fibres and probably a few smooth muscular fibres. They pass off from the capsule of Malpighi and the fibrous coat at right angles, very soon branch, interlace, and unite with each other, becoming smaller and smaller, until they measure from $\frac{1}{250}$ to $\frac{1}{60}$ of an inch. As we should expect from the very variable size of the trabeculæ, the dimensions as well as the form of the cavities are exceedingly irregular. This fibrous net-work serves as a skeleton or a support for the softer and more delicate parts.

FIG. 142.—*Malpighian bodies of the spleen of the pig.* (Frey.)

a, an artery, with its branches (*b*, *b*); *c*, *c*, *c*, Malpighian bodies.

Malpighian Bodies.—In the very elaborate work on the spleen, by Malpighi, is a full account of the closed follicles, which have since been called the Malpighian bodies. They are sometimes called the splenic corpuscles or glands. They are in the form of rounded or slightly ovoid corpuscles, about $\frac{1}{50}$ of an inch in diameter, consisting of a delicate membrane, generally homogeneous, but sometimes faintly striated, with semifluid contents. In their form, size, and structure, they bear a close resemblance to the closed follicles of the small intestine. The investing membrane has no epithelial lining, and the contents consist of an albuminoid liquid, with numerous small, nucleated cells and a few free nuclei. The cells measure from $\frac{1}{3000}$ to $\frac{1}{2500}$ of an inch in diameter. Both the cells and the free nuclei of the splenic corpuscles bear a close resemblance to cells and nuclei found in the spleen-pulp. The corpuscles are surrounded by blood-vessels, which send branches into the interior, to form a delicate capillary plexus.

The number of the Malpighian corpuscles in a spleen of ordinary size has been estimated by Sappey at about ten thousand. They are readily made out in the ox and sheep but are frequently not to be discovered in the human subject. In about forty examinations, in man, Sappey found them in only four; but in these they presented the same characters as in the ox and the sheep, and resisted decomposition for twelve days, showing that it is not necessary to have recourse to perfectly fresh specimens to discover them if they exist. Kölliker notes the fact that they are often absent in the human subject when death has taken place from disease or after long abstinence. He believes that they are nearly always to be found in perfectly healthy persons. The occasional absence of these bodies constitutes another point of resemblance to the solitary glands of the small intestine.

The relations of the Malpighian bodies to the arterial branches distributed throughout the spleen are peculiar. In specimens in which these corpuscles are easily made out, if a thin section be made and the spleen-pulp be washed away by a stream of water, the corpuscles may be seen attached in some parts to the sides of the vessels, in others lying in the notch formed by the branching of a vessel, and in others attached to an extremity of an arterial twig, the vessel then breaking up into plexuses surrounding each corpuscle. According to Sappey, the corpuscles are attached to arteries measuring from $\frac{1}{80}$ to $\frac{1}{60}$ of an inch or less in diameter. When the artery is enclosed in its fibrous sheath, the corpuscles are applied to the sheath, but, in the smallest arteries, they are attached to the walls of the vessels. The attachment of the Malpighian bodies to the vessels is very firm, and they cannot be separated without laceration of the membranes.

Spleen-pulp.—With regard to the constitution of the spleen-pulp, there is considerable diversity of opinion. While anatomists and physiologists are pretty generally agreed concerning the structure and relations of the Malpighian bodies, some minutely describe cells in the pulp, the existence of which is denied by others of equal authority. The pulp, however, contains the essential elements of the spleen, and an accurate knowledge of all the structures contained in it could hardly fail to throw some light on its function; but there is so little that is definitely known of either the anatomy or the physiology of the spleen, that we shall refrain from discussing the views of different authors, referring the reader for full information upon these points to elaborate works upon general anatomy.

The spleen-pulp is a dark, reddish, semifluid substance, its color varying in intensity in different specimens. It is so soft that it may be washed by a stream of water from a thin section, and it readily decomposes, becoming then nearly fluid. It is contained in the cavities bounded by the fibrous trabeculæ, and it contains itself numerous microscopic bands of fibres arranged in the same way. It surrounds the Malpighian bodies, contains the terminal branches of the blood-vessels, and probably the nerves and lymphatics. Upon microscopical examination, it presents numerous free nuclei and cells like those described in the Malpighian bodies; but the nuclei are here relatively much more abundant. In addition are found, blood-corpuscles (white and red) some natural in form and size and others more or less altered, with pigmentary granules, both free and enclosed in cells. Anatomists have attached a great deal of importance to large vesicles enclosing what have been supposed by some to be blood-corpuscles, and by others to be pigmentary corpuscles. The state of our knowledge upon these points, however, is very unsatisfactory. Some authorities deny the existence of the so-called blood-corpuscle-containing cells. We shall abstain from a discussion of these disputed questions, which are at present of a character purely anatomical. All that we can say of the spleen-pulp is, that it contains cells, nuclei, blood-corpuscles, and pigmentary granules, with a yellowish-red fluid, and that it is intersected with microscopic trabeculæ of fibrous and muscular tissue and a delicate net-work of blood-vessels. It is difficult to determine whether the blood-corpuscles come from vessels that have been divided in making our preparations or are really free in the pulp; or whether the free nuclei are normal or come from cells that have been artificially ruptured.

Vessels and Nerves of the Spleen.—The quantity of blood which the spleen receives is very large in proportion to the size of the organ. The splenic artery is the largest branch of the cœliac axis. It is a vessel of considerable length and is remarkable for its excessively tortuous course. In a man between forty and fifty years of age, the vessel measured about five inches, without taking account of its deflections; and a thread placed on the vessel, so as to follow exactly all its windings, measured a little more than eight inches. The large caliber of this vessel and its tortuous course are interesting points in connection with the great variations in size and situation which the spleen is liable to undergo in health and disease. The artery gives off several branches to the adjacent viscera in its course, and, as it passes to the hilum, it divides into three or four branches, which again divide so as to form from six to ten vessels. These penetrate the substance of the spleen, with the veins, nerves, and lymphatics, enveloped in the fibrous sheath, the capsule of Malpighi. In the substance of the spleen, the arteries branch rather peculiarly, giving off many small ramifications in their course, generally at right angles to the parent trunk. These are accompanied by the veins until they are reduced to from $\frac{1}{80}$ to $\frac{1}{60}$ of an inch in diameter. The two classes of vessels then separate, and the arteries have attached to them the corpuscles of Malpighi. It is also a noticeable fact that the distinct trunks passing in at the hilum have but few inosculations with each other in the substance of the spleen, so that the organ is divided up into from six to ten vascular compartments.

The veins join the fine branches of the arteries in the spleen-pulp and pass out of the spleen in the same sheath. They anastomose quite freely in their larger as well as their smaller branches. Their caliber is estimated by Sappey as about twice that of the arteries. This author regards the estimates, which have put the caliber of the veins at four or five times that of the arteries, as much exaggerated. The number of veins emerging from the spleen is equal to the number of arteries of supply.

The lymphatics of the spleen are not numerous. By most anatomists, two sets of vessels have been recognized, the superficial and the deep; but those who have studied the subject practically have found it very difficult to demonstrate the superficial layer. The deep lymphatics have been demonstrated in the capsule of Malpighi, attached to the veins and emerging with them at the hilum. At the hilum, the deep vessels are joined by a few from the surface of the spleen. The vessels, numbering five or six, then pass into small lymphatic glands and empty into the thoracic duct opposite the eleventh or twelfth dorsal vertebra. It was an old idea that the lymphatics were the excretory ducts of the spleen; but this is a speculation which does not demand discussion at the present day.

The nerves of the spleen are derived from the solar plexus. They follow the vessels in their distribution and are enclosed with them in the capsule of Malpighi. They are distributed ultimately in the spleen-pulp, but nothing definite is known of their mode of termination. We have already referred to the fact that, when these nerves are galvanized, the non-striated muscles in the substance of the spleen are thrown into contraction.

Some Points in the Chemical Constitution of the Spleen.—Very little has been learned with regard to the probable function of the spleen, from the numerous chemical analyses that have been made of its substance. It will therefore be out of place to discuss its chemical constitution very fully, and we shall only refer to certain principles, the existence of which, in the spleen-substance, may be considered as pretty well determined. In the first place, cholesterine has been found to exist in the spleen constantly and in considerable quantity, and the same may be said of uric acid. In addition, chemists have extracted from the substance of the spleen, hypoxanthine, leucine, tyrosine, a peculiar crystallizable substance called, by Scherer, lienine, crystals of hæmatoidine, lactic acid, acetic acid, butyric acid, inosite, amyloid matter, and some indefinite fatty principles. It is difficult, however, to say how far some of these principles are formed by the processes employed for their extraction or are due to morbid action; certainly, physiologists have thus far been unable to connect them with any definite views with regard to the probable function of the spleen.

State of our Knowledge concerning the Functions of the Spleen.—The spleen is almost universal in vertebrate animals; it is an organ of considerable size, and is very abundantly supplied with vessels and nerves; it has a complex structure, unlike that of any of the true glands; its tissue presents a variety of proximate principles; but it has no excretory duct, and no opportunity is afforded for the study of its secretion, except as it may be taken up by the current of blood. It must be admitted, also, that, up to the present time, no definite physiological ideas have followed the elaborate microscopical and chemical examinations of the spleen. There have been only two methods of inquiry, indeed, which have promised any such results: First, a comparison of the blood and lymph going into and coming from the spleen, and an examination of the variations in the volume of the organ during life; and second, a study of the phenomena which follow its extirpation in living animals. A review of the literature of the subject will show that we have gained but little positive information from either of these methods of study.

The condition of the question of the influence of the spleen upon the composition of the blood is well illustrated in the last edition of Longet's elaborate work upon physiology. This author quotes opinions of the highest authorities, based chiefly upon microscopical investigations, some in favor of the view that the blood-corpuscles are destroyed, and others arguing that they are formed in the spleen, while he himself offers no opinion upon the subject. Still, there are certain established points of difference between the blood of the splenic artery and of the splenic vein. There can be little doubt of the fact that the blood coming from the spleen contains a large excess of white corpuscles; but it can by no means be considered as settled that the function of the spleen is to form white blood-corpuscles. In pathology, although great increase in the leucocytes of the blood frequently attends hypertrophy of the spleen, this condition is also observed when the spleen is perfectly healthy.

Diminution in the proportion of red corpuscles in the blood in passing through the spleen, in a very marked degree, has been noted, and this gives color to the supposition that the spleen is an organ for the destruction of the blood-corpuscles; but we know nothing of the importance or significance of this process, and it is not shown that the corpuscles exist in undue quantity in animals after the spleen has been removed. We learn nothing more definite from the fact that the blood of the splenic vein seems to contain an unusual quantity of pigmentary matter. In connection with the marked diminution in the proportion of blood-corpuscles, physiologists have observed a marked increase in albuminoid matters in the blood of the splenic vein.

The significance of the facts just stated is so little understood, that it would seem hardly necessary even to mention them, except as an illustration of the small amount of definite information regarding the functions of the spleen that has resulted from an examination of the blood coming from this organ. We know nothing of any changes effected by the spleen in the constitution of the lymph.

Variations in the Volume of the Spleen.—One of the theories with regard to the function of the spleen, which merits a certain amount of consideration, is that it serves as a diverticulum for the blood, when there is a tendency to congestion of the other abdominal viscera.

It has been shown that the spleen is greatly enlarged in dogs, from four to five hours after feeding, that its enlargement is at its maximum at about the fifth hour, and that it gradually diminishes to its original size during the succeeding twelve hours; but it is not apparent how far these changes are important or essential to the proper performance of the functions of digestion and absorption. Experiments have shown that animals may live, digest, and absorb alimentary principles perfectly well after the spleen has been removed, and this has even been observed in the human subject; and, in view of these facts, it is impossible to assume that the presence of the spleen, as a diverticulum for the blood, is essential to the proper action of the other abdominal organs.

Extirpation of the Spleen.—There is one experimental fact that has presented itself in opposition to nearly every theory advanced with regard to the function of the spleen; which is, that the organ may be removed from a living animal, and yet all the functions of life go on apparently as before. The spleen is certainly not necessary to life, nor, as far as we know, is it essential to any of the important general functions. It has been removed over and over again from dogs, cats, and even from the human subject, and its absence is attended with no constant and definite changes in the phenomena of life. If it act as a diverticulum, this function is not essential to the proper operation of the organs of digestion and absorption; and, if its office be the destruction or the formation of the blood-corpuscles, the formation of leucocytes, of uric acid, of cholesterine, or of any excrementitious matter, there are other organs which may perform these functions. What renders this question even more obscure is the fact that we have no knowledge of any constant modifications in the size or the functions of other organs as a consequence of removal of the spleen. This is not surprising, however, when we reflect that one kidney may accomplish the function of urinary excretion after the other has been removed, and that the single organ which remains does not present enlargement of the Malphigian bodies and the convoluted tubes.

There are certain phenomena that sometimes follow removal of the spleen from the lower animals, which are curious and interesting, even if they do not afford much positive information. Extirpation of this organ is an old and a very common experiment. In the works of Malpighi, published in 1687, we find an account of an experiment on a dog, in which the spleen was destroyed, and the operation was followed by no serious results. Since then it has been removed so often, and the experiments have been so universally negative in their results, that it is hardly necessary to cite authorities upon the subject. There are numerous instances, also, in which it has been in part or entirely removed from the human subject, which it is unnecessary to refer to in detail; but, in nearly every case, when there was no diseased condition to complicate the observation, the results have been the same as in experiments on the inferior animals.

One of the phenomena following extirpation of the spleen, to which we desire to call attention, is a modification of the appetite. Great voracity in animals after removal of the spleen was noted by the earlier experimenters, and this formed the basis of some of their extravagant theories. Later experimenters have observed this change in the appetite and have noted that digestion and assimilation do not appear to be disturbed, the animals becoming unusually fat. Prof. Dalton has also observed that the animals, particularly dogs, sometimes present a remarkable change in their disposition, becoming unnaturally ferocious and aggressive. We have frequently observed these phenomena after removal of the spleen; and, in the following experiment, performed in 1861, they were particularly marked:

The spleen was removed from a young dog weighing twenty-two pounds, by the ordinary method; viz., making an incision into the abdominal cavity in the linea alba, drawing out the spleen, and exsecting it after tying the vessels. Before the operation the dog presented nothing unusual, either in his appetite or disposition. The wound healed rapidly, and, after recovery had taken place, the animal was fed moderately once a day. It was noticed, however, that the appetite was excessively voracious; and the dog became so irritable and ferocious that it was dangerous to approach him, and it became necessary to separate him from the other animals in the laboratory. He would eat refuse from the dissecting-room, the flesh of dogs, fæces, etc. On February 11, 1861, about six weeks after the operation, having been well fed twenty-four hours before, the dog was brought before the class at the New Orleans School of Medicine, and he ate a little more than four pounds of beef-heart, nearly one fifth of his weight. This he digested perfectly well, and the appetite was the same upon the following day. This dog had a remarkably sleek and well-nourished appearance.

The above is a striking example of the change in the appetite and disposition of animals after extirpation of the spleen; but these results are by no means invariable. We have often removed the spleen from dogs and kept the animals for months without observing any thing unusual; and, on the other hand, we have observed the change in disposition and the development of an unnatural appetite, in animals after removal of one kidney. These effects were also very well marked in an animal with biliary fistula, that lived for thirty-eight days. In the latter instance, the voracity could be explained by the disturbance in digestion and assimilation produced by shutting off the bile from the intestine; but these phenomena occurring after removal of one kidney, which appeared to have no effect upon the ordinary functions, are not so readily understood. We have observed both increase in the appetite and the development of extraordinary ferocity after extirpation of one kidney almost invariably, since our attention has been directed to this point; and, in the experiments of which records were preserved, these effects were very marked. In one, a dog lived for nearly two years with one kidney and was finally killed. The appetite was voracious and depraved. He would eat dogs' flesh greedily. In another, death took place in convulsions, forty-three days after removal of one kidney, the animal having apparently recovered from the operation. This dog was very ferocious, had an extraordinary appetite, and would eat fæces, putrid dogs' flesh, etc., which the other dogs in the laboratory would not touch. The other dog entirely recovered from the operation of removing one kidney and presented the same phenomena.

In view of the above facts, it must be admitted that removal of the spleen in the lower animals and the human subject has thus far demonstrated nothing, except that this part is not essential to the proper performance of the vital functions. The voracity which occasionally follows the operation in animals is one of the phenomena, like the increase in the size of animals after castration, for which physiologists can offer no satisfactory explanation.

It is evident from the foregoing considerations that, notwithstanding the great amount of literature upon the anatomy and functions of the spleen, physiologists have no definite knowledge of any important office performed by this organ. With this conclusion, we pass to a consideration of the other ductless glands, the physiology of which is, unfortunately, even more unsatisfactory.

Suprarenal Capsules.

The theories that have been advanced with regard to the function of the suprarenal capsules have not, as a rule, been based upon anatomical investigations, but have taken their origin from pathological observations and experiments upon living animals. This fact detracts from the physiological interest attached to the structure of these bodies, and we shall consequently treat of their anatomy very briefly.

The suprarenal capsules, as their name implies, are situated above the kidneys. They are small, triangular, flattened bodies, situated behind the peritoneum, and capping the kidneys at the anterior portion of their superior ends. The left capsule is a little larger than the right, and is rather semilunar in form, the right being more nearly triangular. Their size and weight are very variable in different individuals. Of the different estimates given by anatomists, we may state, as an average, that each capsule weighs about one hundred grains. They are about an inch and a half in length, a little less in width, and a little less than one-fourth of an inch in thickness.

The weight of the capsules, in proportion to that of the kidneys, presents great variations at different periods of life; and they are so much larger in the fœtus than after birth, that some physiologists, in the absence of any reasonable theory of their function in the adult, have assumed that their office is chiefly important in intra-uterine life. Meckel states that they are easily distinguished in the fœtus of two months; at the end of the third month, they are a little larger and heavier than the kidneys; they are equal in size to the kidneys (though a little lighter) at four months; and, at the beginning of the sixth month, they are to the kidneys as two to five. In the fœtus at term, the proportion is as one to three, and in the adult, as one to twenty-three. It was asserted by some of the older writers, that the capsules are larger in the negro than in the white races, but Meckel states that, although he had observed this in a negress, he saw nothing of it in dissecting a negro. This observation did not have much significance at that time; but since it has been supposed that the suprarenal capsules have some function in connection with the formation of pigment, authors have quoted it as important.

The color of the capsules is whitish-yellow. They are completely covered by a thin, fibrous coat, which penetrates their interior, in the form of trabeculæ. Upon section, they present a cortical and a medullary substance. The cortex is yellowish, from $\frac{1}{25}$ to $\frac{1}{12}$ of an inch in thickness, surrounding the capsule entirely, and constituting about two-thirds of its substance. The medullary substance is whitish, very vascular, and is remarkably prone to decomposition, so that it is desirable to study the anatomy of these bodies in specimens that are perfectly fresh.

Structure of the Suprarenal Capsules.

Cortical Substance.—The cortical substance is divided into two layers. The external is pale-yellow, and is composed of closed vesicles, rounded or ovoid in form, containing an albuminoid fluid, cells, nuclei, and fatty globules. This layer is very thin. The greater part of the cortical substance is of a reddish-brown color and is composed of closed tubes. On making thin sections through the cortical substance previously hardened in chromic acid and rendered clear by means of glycerine, numerous rows of cells are seen, arranged with great regularity, and extending, apparently, from the investing membrane to the medullary substance. On studying these sections with a high magnifying-power, it is evident that the cells are enclosed in tubes measuring from $\frac{1}{1000}$ to $\frac{1}{325}$ of an inch in diameter. The cells are granular, with a distinct nucleus and nucleolus, and a variable number of oil-globules. They measure from $\frac{1}{1750}$ to $\frac{1}{1000}$ of an inch in diameter. Between the tubes of the cortical substance, are bands of fibrous tissue, connected with the covering of the capsule.

Medullary Substance.—The medullary substance is much paler and more transparent than the cortex. In its centre are numerous openings, marking the passage of its venous sinuses. It is penetrated in every direction by excessively delicate bands of fibrous tissue, which enclose blood-vessels, nerves, and numerous elongated, closed vesicles, containing cells, nuclei, and granular matter. These vesicles, $\frac{1}{80}$ of an inch long and about $\frac{1}{400}$ of an inch broad, have been demonstrated in the ox and in the human subject. The cells in the human subject are from $\frac{1}{1700}$ to $\frac{1}{1200}$ of an inch in diameter. They are isolated with difficulty and are very irregular in their form. The nuclei measure about $\frac{1}{2500}$ of an inch. The medullary substance is peculiarly rich in vessels and nerves.

Vessels and Nerves.—The blood-vessels going to the suprarenal capsules are very numerous and are derived from the aorta, the phrenic artery, the cœliac axis, and the renal artery. Sometimes as many as twenty distinct vessels penetrate each capsule. In the cortical substance, the capillaries are arranged in elongated meshes, anastomosing freely, and surrounding the tubes, but never penetrating them. In the medullary substance, the meshes are more rounded, and here the vessels form a very rich capillary plexus. Two large veins pass out, to empty, on the right side, into the vena cava, and on the left, into the renal vein. Other smaller veins empty into the vena cava, the renal, and the phrenic veins.

The nerves are very numerous and are derived from the semilunar ganglia, the renal plexus, the pneumogastric, and the phrenic. Kölliker mentions that he has counted, in the human subject, thirty-three nervous trunks entering the right suprarenal capsule. The nerves probably pass directly to the medullary substance, but here their mode of distribution is unknown. In the medullary matter, however, are two ganglia, characterized by nerve-cells of the ordinary form, and situated close to the central vein.

Nothing whatever is known of the lymphatics of the suprarenal capsules, and the existence of these vessels, even, is doubtful.

Chemical Reactions of the Suprarenal Capsules.—A few years ago, M. Vulpian discovered in the medullary portion of the suprarenal capsules a peculiar substance, soluble in water and in alcohol, which gave a greenish reaction with the salts of iron and a peculiar rose-tint on the addition of iodine. He could not determine the same reaction with extracts from any other parts. Later, in conjunction with M. Cloez, he discovered hippuric and taurocholic acid in the capsules of some of the herbivora. Other researches have been made into the chemistry of these bodies, but without results of any great physiological importance.

State of our Knowledge concerning the Functions of the Suprarenal Capsules.

In 1855, the late Dr. Addison, of Guy's Hospital, published a remarkable memoir upon a peculiar disease which he had found connected with disorganization of the suprarenal capsules. This disease, sometimes called Addison's disease, is characterized by bronzing of the skin and is accompanied by serious disorders in nutrition. It was supposed to be invariably fatal. The peculiar discoloration of the surface, attended with disorganization of the suprarenal capsules, led physiologists to suppose that, perhaps, these bodies had some function connected with the formation of pigment; and, following the publication of Dr. Addison's memoir, we find quite a number of experiments upon animals, consisting chiefly in extirpation of the capsules. Before this time, there had been no reasonable theory, even, of the probable function of these bodies. As our first ideas of the relations of the suprarenal capsules to the formation of pigment were derived from cases of disease, it may not be out of place to consider briefly whether there be any invariable and positive connection between structural change in these organs and the affection known under the name of bronzed skin.

In the memoir by Dr. Addison, are reported eleven cases of anæmia, accompanied with bronzing of the skin, terminating fatally, and found, after death, to be attended with extensive disorganization of the suprarenal capsules. The reports of these cases attracted a great deal of attention among physiologists as well as pathologists. A year later, Prof. I. E. Taylor, of Bellevue Hospital, reported seven cases of bronzed skin, in two of which the diagnosis of disease of the suprarenal capsules was verified by post-mortem examination. Attention now being directed to this peculiar condition of the system, accompanied with discoloration of the skin, numerous cases were reported from time to time, but some of them did not fully carry out the views of Dr. Addison. Perhaps the most extensive collection of cases taken from a great number of authorities is given by Dr. Greenhow, in his work upon Addison's disease. Dr. Greenhow is apparently convinced that the connection between the constitutional symptoms and discoloration of the skin, described by Addison, and disorganization of the suprarenal capsules is well established. He reports one hundred and ninety-six cases; and, out of these, he selects one hundred and twenty-eight, as fair representatives of Addison's disease. There are several cases (ten) in which there was bronzing of the skin, the suprarenal capsules being perfectly healthy; but in only one of these were there any of the characteristic constitutional symptoms. There are twenty-two cases cited of cancer of the suprarenal capsules, not one of which presented the characteristic constitutional symptoms, only seven presenting some slight discoloration of the skin. Without discussing this subject more fully, it seems justifiable to adopt the opinion, entertained by many pathologists, that there is a connection between bronzed skin accompanied with certain grave constitutional symptoms, and disorganization of the suprarenal capsules, which is frequent but not invariable; but it is not established that the destruction of the capsules stands in a causative relation to the discoloration or to the constitutional disturbance. It is more interesting to us, however, to know that the investigations into these diseased conditions have developed little or nothing of importance concerning the physiology of the supra-renal capsules.

Extirpation of the Suprarenal Capsules.—There are two important questions to be settled by the removal of the suprarenal capsules from living animals. The first is, whether or not these organs are essential to life; and the second, to determine the consequences of their removal, as exhibited in modifications of the animal functions.

Are the suprarenal capsules essential to life? This question can be answered in a very few words. Dr. Brown-Séquard, in his first experiments, removed sometimes one and sometimes both capsules in rabbits, Guinea-pigs, dogs, and cats, and the animals died in the course of two or three days. He also noted several peculiar results, such as turning, and contraction of the pupil, when one capsule had been extirpated, and the development of peculiar crystals in the blood. M. Gratiolet repeated these experiments and ascertained that the left capsule could be removed with impunity, while extirpation of the right was always fatal. M. Philipeaux added a number of observations, experimenting chiefly upon rats and taking great care to disturb the adjacent organs as little as possible. As the result of these experiments, he concluded that the capsules are not essential to life. Of four rats operated upon in this way, three died, as Philipeaux supposed, of cold, the first in nine days, the second in twenty-three days, and the third in thirty-four days. One was alive and well when the report was made, although the capsules had been removed for forty-nine days. In such a question as this, negative experiments are of little account; and the instances in which animals have recovered and lived perfectly well after removal of both suprarenal capsules show conclusively that they are not essential to life. Death has probably been due, in most of the experiments, to injury of the semilunar ganglia, and it is probably on account of the greater injury, from the situation of the capsule, produced by operating on the right side, that the removal of the capsule of that side has been more generally fatal. It is not necessary to take account, in this connection, of the contraction of the pupil, "turning" and other symptoms referable to the nervous system, which have sometimes followed these operations. These phenomena are undoubtedly due to injury of adjacent parts, and not to extirpation of the capsules. The only remaining question to determine is whether the capsules have any thing to do with the formation or change of pigment. Notwithstanding the assertion of Dr. Brown-Séquard, that flakes of pigment and blood-crystals differing from those developed in normal blood are found in animals deprived of the suprarenal capsules, this view is adopted by a few physiological authorities. In view of these facts, and in the absence of comparative examinations of the blood going to the suprarenal capsules by the arteries and returned from them by the veins, it is impossible to assign any definite function to these bodies, and it is certain that they are not essential to life. Their greater relative size before birth has led to the supposition that they might have an important office in intra-uterine life, but this is a pure hypothesis, based upon no positive knowledge.

Thyroid Gland.

The history of this gland belongs almost exclusively to descriptive anatomy, and its only physiological interest is in the similarity of its structure to that of the other ductless glands. It has no excretory duct. It is attached to the lower part of the larynx, following it in its various movements. Its color is brownish-red. The anterior face is convex and is covered by certain of the muscles of the neck. The posterior surface is concave and is applied to the larynx and trachea. It is formed of two lateral lobes, with a rounded, thickened base below, and a long, pointed extremity extending upward, connected by an isthmus. Each of these lobes is about two inches in length, three-quarters of an inch in breadth, and about the same in thickness at its thickest portion. The isthmus connects the lower portion of the lateral lobes. It covers the second and third tracheal rings and is about half an inch wide and one-third of an inch thick. From the left side of the isthmus, and sometimes from the left lobe, is a portion projecting upward, called the pyramid. The weight of the thyroid gland, according to Sappey, is from three hundred and fifty to three hundred and eighty grains. It is usually stated by anatomical writers that it is relatively larger in the fœtus and in early life than in the adult; but Sappey, from his own researches, is disposed to believe that its weight, in proportion to the weight of the adjacent organs, does not vary with age. It is a little larger and more prominent in the female than in the male.

Structure of the Thyroid Gland.—The thyroid gland is covered with a thin but resisting coat of ordinary fibrous tissue, which is loosely connected with the surrounding parts. From the internal surface of this membrane, are numerous fibrous bands, or trabeculæ, giving off, as they pass through the gland, secondary trabeculæ, and then subdividing until they become of microscopic size. By this arrangement, the gland is divided up into communicating cells, like a sponge. These bands are mingled with numerous small elastic fibres. Throughout the substance of the gland, lodged in the meshes of the trabeculæ, are numerous rounded or ovoid closed vesicles, measuring from $\frac{1}{600}$ to $\frac{1}{250}$ of an inch. These are formed of a structureless membrane, and they are lined by a single layer of pale, granular, nucleated cells, from $\frac{1}{3000}$ to $\frac{1}{2000}$ of an inch in diameter. The layer of cells sometimes lines the vesicle completely, sometimes it is incomplete, and sometimes it is wanting. The contents of the vesicles are a clear, yellowish, slightly viscid, albuminoid fluid, with a few granules, pale cells, and nuclei. Robin has described in these vesicles curiously-shaped, translucent, feebly-refracting, colorless bodies which he has called sympexions; but there is little known of their constitution or properties. The vesicles are arranged in little collections or lobes, with the great veins passing between them.

Vessels and Nerves.—The blood-vessels of the thyroid gland are very numerous, this organ being supplied by the superior and inferior thyroid arteries and sometimes by a branch of the innominata. The arteries break up into a close capillary plexus, surrounding the vesicles with a rich net-work, but never penetrating their interior. The veins are large, and, like the hepatic veins, they are so closely adherent to the surrounding tissue that they do not collapse when cut across. The veins emerging from the gland form a plexus over its surface and the surface of the trachea, and they then go to form the superior, middle, and inferior thyroid veins. The nerves are derived from the pneumogastric and the cervical sympathetic ganglia. The lymphatics are numerous but are difficult to inject. The exact distribution of the nerves and the origin of the lymphatics are not well understood.

State of our Knowledge concerning the Functions of the Thyroid Gland.—It is generally admitted that the thyroid gland may be removed from animals without interfering with any of the vital functions; and this, taken in connection with the fact that it is so often diseased in the human subject without producing any general disturbance, shows that its function cannot be very important. Nothing of importance has been learned from a chemical analysis of its substance. The blood of the thyroid veins has been analyzed, but the changes in its composition in passing through the gland are slight and indefinite. An instance is quoted by Longet of periodical enlargement of the gland in a female during menstruation, but there is no evidence that this is of constant occurrence.

Thymus Gland.

The anatomy of the thymus assimilates it to the ductless glands, but its function, whatever it may be, is confined to early life. In the adult the organ is wanting, traces, only, of fibrous tissue, with a little fat, existing after puberty in the situation previously occupied by this gland. As there never has been a plausible theory, even, of the function of this organ, the existence of which is confined to the first two or three years of life, we shall abstain from all discussions with regard to minute points in its anatomy, and give a simple sketch of its structure, as compared with the ductless glands already considered.

The thymus appears at about the third month of fœtal life, and it gradually increases in size until about the end of the second year. It then undergoes atrophy, and it disappears almost entirely at the age of puberty. It is situated partly in the thorax and partly in the neck. The thoracic portion is in the anterior mediastinum, resting upon the pericardium, extending as low as the fourth costal cartilage. The cervical portion extends upward as far as the lower border of the thyroid gland. The whole gland is about two inches in length, one and a half inch broad at its lower portion, and about one-quarter of an inch thick. Its color is grayish, with a slightly rosy tint. It is usually in the form of two lateral lobes lying in apposition in the median line, although sometimes there exists but a single lobe. It is composed of numerous lobules held together by fibrous tissue.

The proper coat of the thymus is a delicate fibrous membrane, sending processes into the interior of the organ. Its fibrous structure, however, is loose, so that the lobules can be separated with little difficulty. Portions of the gland may be, as it were, unravelled, by loosening the interstitial fibrous tissue. In this way it will be found to be composed of numerous little lobular masses attached to a continuous cord. This arrangement is more distinct in the inferior animals of large size than in man. The lobules are composed of rounded vesicles, from ten to fifteen in number, and from $\frac{1}{125}$ to $\frac{1}{40}$ of an inch in diameter. The walls of these vesicles are thin, finely granular, and excessively fragile. The vesicles contain a small quantity of an albuminoid fluid, with cells and free nuclei. The cells are small and transparent, and the nuclei, spherical, relatively large, and containing from one to three nucleoli. The free nuclei are also rounded and contain several distinct nucleoli. These vesicles are easily

FIG. 143.—*Unravelled thymus from the calf; natural size.* (Kölliker.)
a, a, cord of the thymus; *b, b, b,* lobules; *c,* small nodules attached to the cord.

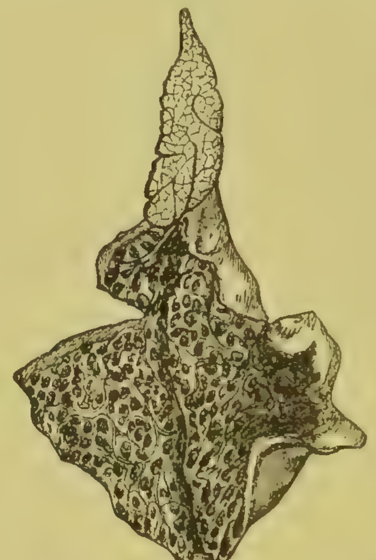


FIG. 144.—*Half of the human thymus, laid open in its lower portion.* (Kölliker.)

ruptured, when their contents exude in the form of an opalescent fluid, sometimes called the thymic juice.

Anatomists are somewhat divided in their opinions with regard to the structure of the central cord and the lobules. Some adopt the view advanced by Sir Astley Cooper, that the cord has a central canal connected with cavities in the lobules; while others believe that the cavities thus described are produced artificially, by the processes employed in anatomical investigation. The latter opinion is the latest and is probably correct.

The blood-vessels of the thymus are numerous, but their caliber is small, and the gland is not very vascular. They are derived chiefly from the internal mammary artery, a few coming from the inferior thyroid, the superior diaphragmatic, or the pericardial. They pass between the lobules, surround and penetrate the vesicles, and form a capillary plexus in their interior. The vesicles, in this respect, bear a certain resemblance to the closed follicles of the intestine. The veins are also numerous, but they do not follow the course of the arteries. The principal vein emerges at about the centre of the gland posteriorly, and it empties into the left brachio-cephalic. Other small veins empty into the internal mammary, the superior diaphragmatic, and the pericardial. A few nervous filaments from the sympathetic system surround the principal thymic artery and penetrate the gland. Their ultimate distribution is uncertain. The lymphatics are very numerous.

Inasmuch as the thymus is peculiar to early life, one of the most interesting points in its anatomical history relates to its mode of development. This, however, does not present any great physiological importance and is fully treated of in works upon anatomy.

Pituitary Body and Pineal Gland.

These little bodies, situated at the base of the brain, are quite vascular, contain closed vesicles and but few nervous elements, and are sometimes classed with the ductless glands. Physiologists have no idea of their function.

The pituitary body is of an ovoid form, a reddish-gray color, weighs from five to ten grains, and is situated on the sella turcica of the sphenoid bone. It is said to be larger in the fœtus than in the adult, and in fœtal life it has a cavity communicating with the third ventricle. This little body has been studied by M. Grandry, in connection with the suprarenal capsules. He regards it as essentially composed of closed vesicles, with fibres of connective tissue and blood-vessels. The vesicles measure from $\frac{1}{375}$ to $\frac{1}{125}$ of an inch in diameter. They are formed of a transparent membrane, containing irregularly polygonal, nucleated cells, and free nuclei. The cells are from $\frac{1}{2500}$ to $\frac{1}{1700}$ of an inch in diameter. The nuclei are distinct, with a well-marked nucleolus, and measure about $\frac{1}{5000}$ of an inch. Capillary vessels surround these vesicles without penetrating them. M. Grandry did not observe either nerve-cells or fibres between the vesicles. In old subjects he found the peculiar concretions (sympexions) already described as existing in the thyroid gland.

The pineal gland is situated just behind the posterior commissure of the brain, between the nates, and is enclosed in the velum interpositum. It is of a conical shape, one-third of an inch in length, and of nearly the color of the pituitary body. It is connected with the base of the brain by several delicate commissural peduncles. It presents a small cavity at its base, and frequently it contains in its substance little calcareous masses, composed of phosphate and carbonate of lime, phosphate of magnesia and ammonia, and a small quantity of organic matter. It is covered with a fibrous envelope, which sends processes into its interior. As the result of the researches of M. Grandry, it has been found to present a cortical substance, entirely analogous in its structure to the pituitary body, and a central portion, composed of the ordinary nervous elements found in the gray matter of the brain. Its structure is regarded by Grandry as very like that of the medullary portion of the suprarenal capsules.

It is difficult to classify organs, of the function of which we are entirely ignorant; but the structure of the little bodies just described certainly resembles that of the ductless glands. We have indicated their anatomy merely to show that their function is probably analogous to that of other organs of the same class.

CHAPTER XV.

NUTRITION—ANIMAL HEAT.

Nature of the forces involved in nutrition—Definition of vital properties—Life, as represented in development and nutrition—Principles which pass through the organism—Principles consumed in the organism—Development of power and endurance by exercise (training)—Formation and deposition of fat—Conditions under which fat exists in the organism—Physiological anatomy of adipose tissue—Conditions which influence nutrition—Products of disassimilation—Animal heat—Limits of variation in the normal temperature in man—Variations with external temperature—Variations in different parts of the body—Variations at different periods of life—Diurnal variations—Relations of animal heat to digestion—Influence of defective nutrition and inanition—Influence of exercise, mental exertion, and the nervous system, upon the heat of the body—Sources of animal heat—Connection of the production of heat with nutrition—Seat of the production of animal heat—Relations of animal heat to the different processes of nutrition—Relations of animal heat to respiration—Exaggeration of the animal temperature in particular parts after division of the sympathetic nerve and in inflammation—Intimate nature of the calorific processes—Equalization of the animal temperature.

NUTRITION proper, in the light in which we propose to consider it in this chapter, is the process by which the physiological decay of the tissues and fluids of the body is compensated by the appropriation of new matter. All of the physiological processes that we have thus far studied, including circulation, respiration, alimentation, digestion, absorption, and secretion, are to be regarded as means directed to a single end; and the great function, to which all the others are subservient, is the general process of nutrition.

The nature of the main forces involved in nutrition, be it in a highly-organized part, like the brain or muscles, or in a tissue called extra-vascular, like the cartilages or nails, is unknown. The phenomena attending the general process, however, have been studied most carefully, and certain important positive results have been attained; but we really find no more satisfactory explanation of the nature of the causative force of nutrition in the doctrines of to-day than in the speculative theories of the ancients.

We can hardly realize the vast extent of the problem of nutrition from a review of the functions which we have already considered. We have seen that the blood contains all the elements that enter into the composition of the tissues and secretions, either identical with them in form and composition, as is the case with the inorganic principles, or in a condition which allows of their transformation into the characteristic principles of the tissues, as we see in the organic substances proper. These materials are supplied to the tissues, in the required quantity, through the circulatory apparatus; and oxygen, which is immediately indispensable to all the operations of life, is introduced by respiration. The great nutritive fluid, being constantly drawn upon by the tissues for materials for their regeneration, is kept at the proper standard by the introduction of new matter into the system in alimentation, its elaborate preparation by digestion, and its appropriation by the fluids by absorption. Many of these processes require the action of certain secretions. The introduction of new matter, so essential to the continuance of the phenomena of life, is demanded, on account of the change of the substance of the tissues into what we call effete matter; and this is discharged from the animal organism, to be appropriated by vegetables, and thus maintain the equilibrium between these two great kingdoms in Nature.

What is it that causes the parts of a living animal organism to undergo change into effete matter, incapable of any further animal functions; and what is it that gives to these parts the power of self-regeneration, when new matter is presented under proper conditions?

These questions are the physiological *ignis fatuus*, which, it is to be feared, will forever elude the grasp of scientific inquiry. They constitute one of the great mysteries ever present in the mind of the student of Nature, and one, the grandeur of which is so immense that it is a problem with which our intelligence can scarcely grapple. Its greatness is commensurate with that of the question of the soul, and its relations to the finite and the infinite; a question which philosophers have been constrained either to admit upon the faith of revelation or to hopelessly abandon. Little if any real progress is to be made by endeavoring to cover the inscrutable problem of life with a simplicity entirely artificial. This will always be attractive, and, to a certain extent, satisfactory to the minds of those unacquainted with the details of natural laws or willing to admit speculative theories upon subjects concerning which it is impossible, in the present condition of science, to have any positive information; and, if generally admitted by biological students, it would carry our science back to the dark periods in its history, when the study of Nature was confined to speculation, and there existed no knowledge based upon the direct observation of phenomena. A new name, arbitrarily applied to organic matter, without any addition to its physiological history, does not advance our definite knowledge. For example, it has long been known that certain nitrogenized constituents of the organism, classed collectively as organic principles, seem to give to the tissues their property of self-regeneration and development. It may seem to those not engaged in scientific inquiry that a recital of the wonderful properties of "protoplasm" affords some additional information concerning the phenomena observed in organized bodies; but the true definition of the term leads us back to our former ideas of the so-called vital properties of organic matters.

It is a well-established fact that, while nearly all of the tissues undergo disassimilation, or conversion into effete matter, during their physiological decay in the living organism, others, like the epidermis and its appendages, are gradually desquamated, and, when once formed, do not pass through any farther changes. The whole question of the essence and nature of the nutritive property or force resolves itself into vitality. Life is always attended with what we know as the phenomena of nutrition, and nutrition does not exist except in living organisms. When we can state positively what is life, we shall know something of nutrition. At present, physiologists have been able to define life only by a recital of certain of its invariable and characteristic attendant conditions; and yet there are few, if any, definitions of life—regarding it as the sum of the phenomena peculiar to living organisms—that are not open to grave objections.

If we regard life as a principle, it stands in the relation of a cause to the vital phenomena; if we regard it as the totality of these phenomena, it is an effect.

If we study the development of a fecundated ovum, life seems to be a principle, giving the wonderful property of appropriating matter from without, until the germ becomes changed, from a globule of microscopic size and an apparently simple structure, into a complete organism with highly-elaborated parts. This organism has a definite form and size, a definite period of existence, and it produces, at a certain time, generative elements, capable of perpetuating its life in new beings. We may say that an organism dies physiologically because the vital principle, if we admit the existence of such a principle, has a limited term of existence. But, on the other hand, the fully-developed living organism, which we call an animal, presents numerous distinct parts, each endowed with an independent property called vital, that property recognized by Haller in various tissues, under the name of irritability; and it is the coördinated sum of these vitalities that constitutes the perfect being. These are more or less distinct; and we do not commonly observe a sudden and simultaneous arrest of the vital properties in all the tissues, in what we call death. For example, the nerves may die before the muscles, or the muscles, before the nerves. It is also found that vital properties, apparently lost or destroyed, may be made to return; as in resuscitation after asphyxia, or in the restoration of muscular or nervous irritability by injection of blood.

The life of a fecundated ovum is the property which enables it to undergo a certain development when placed under favorable conditions; and, by the surrounding conditions, its development may be arrested, suspended, or modified. The life of a non-fecundated ovum is like that of any ordinary anatomical element.

The life of an anatomical element or tissue in process of development is the property by virtue of which it arrives at its perfection of organization and performs certain defined functions, as far as its organization will permit. This can also be destroyed, suspended, or modified by surrounding conditions.

The life of a perfect anatomical element or tissue is the property which enables it to regenerate itself and perform its functions, subject, also, to modifications from surrounding conditions.

The life of a perfect animal organism is the sum of the vitalities of its constituent parts; but a being may live with the vitality of certain parts abolished or seriously modified, as a man exists and preserves his identity with a limb amputated. Life may continue for a long time without consciousness, or with organs paralyzed or their function destroyed; but certain functions, such as respiration and circulation, are indispensable to the nutrition of all parts, and the vitality of the different tissues is speedily lost when these processes are arrested, and the being then ceases to exist.

These considerations make it evident that it is difficult, if not impossible, to give a single, comprehensive definition of life, a study of the varied phenomena of which constitutes the science of physiology.

The general process of nutrition begins with the introduction of matter from without, called food. It is carried on by the appropriation of this matter by the organism. It is attended with the production of excrementitious principles and the development of certain phenomena that we have not yet studied, the most important of which is the production of heat. We shall have little to say about food, beyond what we have already considered under the head of alimentation, except to classify the alimentary principles with reference to their relations to the general process of nutrition.

Principles which pass through the Organism.

All of the inorganic principles taken in with the food pass out of the organism, generally in the form in which they enter, in the fæces, urine, and perspiration; but it must not be inferred from this fact that they are not useful as constituent parts of the body. Some of these principles, such as water and the chlorides, have very important functions of a purely physical nature. It is necessary, for example, that the blood should contain a certain proportion of the chloride of sodium, this substance modifying and regulating the processes of absorption and probably of assimilation. In addition, however, we find the chlorides as constituent parts of every tissue and organ of the body, and they are so closely united with the nitrogenized principles that they cannot be completely separated without incineration. Those inorganic matters, the function of which is so marked in their passage through the body, are found largely as constituents of the fluids and are less abundant in the solids. They are contained in quantity, also, in the liquid excretions; and any excess over the amount actually required by the system is thrown off in this way. Other inorganic matters are especially important as constituent parts of the tissues, and they are more abundant in the solids than in the fluids. Examples of principles of this class are the salts of lime, particularly the phosphates. These are also in a condition of intimate union with organic matter, and they accompany these principles in all of their so-called vital acts.

If we except certain simple chemical changes, such as the decomposition of the bicarbonates, the inorganic elements of food do not necessarily undergo any modification in the process of digestion. They are generally introduced already in combination with organic matter, and they accompany it in the changes which it passes through in digestion, assimilation by the blood, deposition in the tissues, and the final transformations that result in the various excrementitious matters; so that we find the inorganic principles united with the organic matter of the food as it enters the body, and what seem to be the same principles in connection with the organic excrementitious matters. Between these two extremes, however, are the various operations of assimilation and disassimilation, from which inorganic matter is never absent. As we have not yet taken up fully the connection of the various inorganic matters with nutrition, it will be convenient here to give a brief review of the different individual principles of this class.

Inorganic Principles.

The number of these principles now well established as existing in the human body is about twenty-one. All substances which at any time exist in the body are proximate principles; but some are found in small quantities, are not always present, and apparently have no very important function. These will be passed over rapidly, as well as those which are so intimately connected with some important function as to render their full consideration in connection with that function indispensable. The following is a list of the most important inorganic principles, excluding those which are excrementitious and one or two which are not yet well established:

Table of Inorganic Principles.

	Proximate Principle.	*Where found.*
Gases.	Oxygen.	Lungs and blood.
Gases.	Hydrogen.	Gases of stomach and colon, and blood.
Gases.	Nitrogen.	Lungs, intestinal gases, and blood.
Gases.	Carburetted hydrogen.	Lungs (expired air), intestines.
Gases.	Sulphuretted hydrogen.	Lungs (expired air), intestines.
	Water.	Universal.
	Chloride of sodium.	Universal, except the enamel.
	Chloride of potassium.	Muscles, liver, milk, chyle, blood, mucus, saliva, bile, gastric juice, cephalo-rachidian fluid, and urine.
	Phosphate of lime (basic).	Universal.
	Carbonate of lime.	Bones, teeth, cartilage, internal ear, blood, sebaceous matter, and sometimes the urine.
	Carbonate of soda.	Blood, bone, saliva, lymph, cephalo-rachidian fluid, and urine.
	Carbonate of potassa.	Blood, bone, lymph, and urine.
	Phosphate of magnesia.	Universal.
	Phosphate of soda (neutral).	Universal.
	Phosphate of potassa.	Universal.
	Sulphate of soda.	Universal, except milk, bile, and gastric juice.
	Sulphate of potassa.	Same as sulphate of soda.
	Sulphate of lime.	Blood and fæces.
	Hydrochlorate of ammonia.	Gastric juice, saliva, tears, and urine.
	Carbonate of magnesia.	A trace in the blood and sebaceous matter.
	Bicarbonate of soda.	Blood (Liebig).

Gases.—The gases (oxygen, hydrogen, nitrogen, carburetted hydrogen, and sulphuretted hydrogen) exist both in a gaseous state and in solution in some of the fluids of the body. Oxygen plays a most important part in the function of respiration; but the office of the other gases is by no means so essential. Nitrogen seems to be formed by the system in small quantity and is taken up by the blood and exhaled by the lungs, except during inanition, when the blood absorbs a little from the inspired air. It exists in greatest quantity in the intestinal canal. Carburetted and sulphuretted hydrogen, with pure hydrogen, are found in minute quantities in the expired air and are also found in a gaseous state in the alimentary canal. From the offensive nature of the contents of the large intestine, we should suspect the presence of sulphuretted hydrogen in considerable quantity; but actual analysis has shown that the gas contained in the stomach and intestines, large as well as small, is composed chiefly of nitrogen, with hydrogen and carburetted hydrogen in about equal proportions (five to eleven parts per hundred), and but a trace of sulphuretted hydrogen. With the exception, then, of oxygen and carbonic acid, the latter being an excretion, the gases do not hold an important place among the proximate principles. At all events, their function, whether it be important or not, is but little understood.

Water.—This principle exists in all parts of the body; in the fluids, some of which, as the lachrymal fluid and perspiration, contain little else, and in the hardest structures, as the bones and the enamel of the teeth. In the solids and semisolids it does not exist as water, but it enters into their structure, assuming the consistence by which the tissues are characterized. For example, we have water in the bones, teeth, and even in the enamel, not contained in the interstices of their structure as in a sponge, but incorporated into the substance of the tissue. In these situations, it is essentially water of composition. During the process of nutrition, water is deposited in the tissues with the other nutritive principles, as we have it incorporated in the substance of certain inorganic compounds in the process of crystallization, when it is known in chemistry as water of crystallization. In the interior of the body, water is thus incorporated in the substance of organic matters, which are of indefinite chemical composition and non-crystallizable, and the water enters into their composition, within certain limits, in indefinite proportions, assuming the consistence of the organic substance. As physiologists, studying the organism not from a purely chemical point of view, we must consider water as an integral constituent of the tissues and not as merely absorbed by them.

All the organized structures contain a certain proportion of water, and this is necessary to the performance of all or any of their functions. If a normal muscle be considered as a contracting organ, and a nerve, as a conducting organ, or albumen, as a nutritious element, we must consider water as one of their constituents. It is necessary to the proper form, consistence, and function of these and of all organized structures. In analyses of organic matters, when water is lost or driven off in our manipulations, the principle is not brought near a state of chemical purity, but it is essentially and radically changed.

The quantity of water which each organic substance contains is important; and it is provided that this quantity, though indefinite, shall not exceed or fall below certain limits. The truth of this proposition is made evident from the following facts: In the first place, all organs and tissues must contain a tolerably definite quantity of water to give them proper consistence. The evils of too great a proportion of water in the system, and consequently a diminution of solid elements, are well known to the practical physician. General muscular debility, loss of appetite, dropsies, and various other indications of imperfect nutrition, are among the results of such a condition; while a deficiency of water is immediately made known by the sensation of thirst, which leads to its introduction from without.

The fact that water never exists in any of the fluids, semisolids, or solids, without being combined with inorganic salts, and especially chloride of sodium, is one reason why its proportion in various situations is to a certain extent constant. The presence of these salts influences, in the semisolids at least, the quantity of water entering into their composition, and consequently it regulates their consistence. A very simple experiment shows this with reference to the chloride of sodium. If a piece of muscle be placed in a strong solution of common salt, as in salting meat, it becomes harder and loses a portion of its water of composition; but, if it be exposed to the action of pure water, it absorbs a certain quantity and becomes softer. The nutrient fluid of the muscles during life contains water with just enough saline matter to preserve the normal consistence of the parts. This action of saline matters is even more apparent in the case of the blood-corpuscles. If pure water be added to the blood, these bodies swell up and are finally dissolved; while, if we add a strong solution of salt, they lose water and become shrunken and corrugated. Their natural form and consistence can be restored, however, even after they have been completely dried, by adding water containing about the proportion of salt which exists in the blood-plasma. It seems clear, then, that water is a necessary element of all tissues and is especially important to the proper constitution of organic nitrogenized substances; that it enters into the constitution of these substances, not as pure water, but always in connection with certain inorganic salts; that its proportion is confined within certain limits; and that the quantity in which it exists, in organic nitrogenized substances particularly, is regulated by the quantity of salts which enter, with it, into the constitution of these substances.

The quantities of water which can be driven off by a moderate temperature (212° Fahr.) from the different fluids and tissues of the body vary of course very considerably, according to the consistence of the parts. The following is a list of the quantities in the most important fluids and solids:

Table of Quantities of Water.

		Parts per 1,000.
Solids and semisolids.	In Enamel of the teeth	2
	" Epithelial desquamation	37
	" Teeth	100
	" Bones	130
	" Tendons (Burdach)	500
	" Articular cartilages	550
	" Skin (Weinholt)	575
	" Liver (Frommherz and Gugert)	618
	" Muscles of man (Bibra)	725
	" Ligaments (Chevreul)	768
Liquids.	" Mean of blood of man (Becquerel and Rodier)	780
	" Milk of human female (Simon)	887
	" Chyle of man (Rees)	904
	" Bile	905
	" Urine	933
	" Human lymph (Tiedemann and Gmelin)	960
	" Human saliva (Mitscherlich)	983
	" Gastric juice	984
	" Perspiration	986
	" Tears	990
	" Pulmonary vapor	997

Function of Water.—After what has been stated respecting the condition in which water exists in the body, there remains but little to say concerning its function. As a constituent of organized tissues, it gives to cartilage its elasticity, to tendons their pliability and toughness; it is necessary to the peculiar power of resistance of the bones; and, as we have already seen, it is essential to the proper consistence of all parts of the body. It has other important functions as a solvent. Soluble articles of food are introduced in solution in water. The excrementitious matters, which are generally soluble in water, are dissolved by it in the blood, are carried to the organs of excretion, and are discharged in a watery solution from the body.

Origin and Discharge of Water.—It is evident that a great proportion of the water in the organism is introduced from without, in the fluids and in the watery constituents of all kinds of food; but the theoretical views of some physiologists with regard to the hydrocarbons and their combustion have led to the supposition that water is also formed in the body by a direct union of oxygen and hydrogen. The true way of determining this point is to estimate all the water introduced into the organism, and then to compare this quantity with that which is discharged. The latter estimate, however, presents very great difficulties. As water is continually given off in the form of vapor from the skin and in the expired air, the quantities thus discharged are subject to great variations, dependent upon exercise, temperature, the state of the atmosphere, etc., and even if constant they could be estimated with great difficulty. Experiments upon this point have been undertaken by Sanctorius, Barral, Boussingault, and others, but they are not sufficiently complete to settle the question.

In the present state of our knowledge, we can only say that water is introduced with the fluid and solid elements of food by the stomach, and that it escapes by the urine, fæces, lungs, and skin. There is no direct evidence that water is produced *de novo* in the interior of the body. In the issue of water by the kidneys and skin, it has long been observed that, in point of activity, these two emunctories bear a certain relation to each other. When the skin is inactive, as in cold weather, the kidneys discharge a large quantity of water; and, when the skin is active, the quantity of water discharged by the kidneys is diminished. Certain therapeutical agents, also, can be made to act as diaphoretics, by combining other measures which favor cutaneous action, or as diuretics, by employing measures to diminish the action of the skin.

Chloride of Sodium.—Chloride of sodium is next in importance, as an inorganic proximate principle, to water. It is found in the body at all periods of life, existing, like water, in the ovum. It exists in all the fluids and solids of the body, with the single exception of the enamel of the teeth. In the fluids, it seems to be simply in a state of solution, and it can be recognized by the ordinary tests. In this respect we may class together the chlorides of sodium and potassium.

The quantity of chloride of sodium in the entire body has never been estimated; nor, indeed, has any accurate estimate been made of the quantity contained in the various tissues, for all the chlorides are generally estimated together. It exists in greatest proportion in the fluids, giving to some of them, as the tears and perspiration, a distinctly saline taste. The following table gives an idea of the quantities which have been found in some of the most important of the fluids and solids:

Table of Quantities of Chloride of Sodium.

	Parts per 1,000.
In Blood, human (Lehmann)	4·210
" Chyle (Lehmann)	5·310
" Lymph (Nasse)	4·120
" Milk, human (Lehmann)	0·870
" Saliva, human (Lehmann)	1·530
" Perspiration, human (mean of three analyses, Piutti)	3·433
" Urine (maximum) } Valentin.	7·280
" " (mean) } Valentin.	4·610
" " (minimum) } Valentin.	2·400
" Fæcal matters (Berzelius)	3·010

Function of Chloride of Sodium.—The function of this principle is undoubtedly important, but it is not yet fully understood. It does not seem to enter into the substance of the organized solids and semisolids as an important and essential element, but apparently it exercises its chief function in the fluids. It certainly determines, to a great extent, the quantities of exudations, regulates absorption, and serves to maintain the albuminoids, especially those contained in the blood, in a state of fluidity. Albumen is coagulated by heat with much greater difficulty in a solution of chloride of sodium than when mixed with pure water. A strong solution of common salt is capable of dissolving caseine or of preventing the formation of fibrin. We have already alluded to the fact that it is the chloride of sodium particularly which regulates the quantity of water entering into the composition of the blood-corpuscles, thereby preserving their form and consistence; and that it seems to perform an analogous function with regard to the other semi-solids of the body. As to the general function of this substance, the following proposition of Liebig is adopted by Robin and Verdeil, and a little reflection will show that it is sustained, as far as we know, by the facts:

"Common salt is intermediate in certain general processes, and does not participate by its elements in the formation of organs."

In the first place, the fluids of the body are generally intermediate in their functions, containing nutritious elements, which are destined to be appropriated by the tissues and organs, and worn-out elements, which are to be separated from the body. In the blood and chyle, chloride of sodium is found in greatest abundance. As the nutrition of organs occurs, which consists in the fixation of new proximate principles, chloride of sodium is not deposited in any considerably quantity, but it seems to regulate the general process, at least to a certain extent. In all civilized countries, salt is used extensively as a condiment, and it undoubtedly facilitates digestion by rendering the food more savory and increasing the flow of the digestive fluids; here, likewise, acting simply as an intermediate agent. There is nothing more general among men and animals than this desire for common salt. The carnivora crave it and obtain it in the blood of animals; the herbivora frequent "salt licks" and places where it is found, and relish it when mixed with their food; and by man its use is almost universal. In the domestic herbivora, the effect of a deprivation of this article is very marked and has been made the subject of some very interesting experiments, by Boussingault. This observer experimented upon two lots of bullocks, of three each, all of them, at the time the observations were commenced, being perfectly healthy and in fine condition. One of these lots he deprived entirely of salt, except what was contained in their fodder, while the other was supplied with the usual quantity. No marked difference in the two lots was noticed until between five and six months, when the difference in general appearance was very distinct. The animals receiving salt retained their fine appearance, while the others, though not diminished in flesh, were not so sleek and fine. At the end of a year the difference was very marked. The hides of those which had been deprived of salt were rough and ragged, and their appearance, listless and inanimate, contrasting strongly with the sleek appearance and vivacious disposition of the others. The experiments of Boussingault are the most conclusive that have ever been instituted with regard to the influence of chloride of sodium upon nutrition. They indicate a certain deficiency in the nutrition of animals deprived of it, but not any considerable loss of weight. Before these observations were made, Dailly made analogous experiments upon twenty sheep, which were continued for three months. At the end of that time, the lot which received salt presented a considerable excess of weight (about 22¾ lbs.) over the others.

It is a significant fact that the quantity of chloride of sodium existing in the blood is not subject to variation, but that an excess introduced with the food is thrown off by the kidneys. The quantity in the urine, then, bears a relation to the amount introduced as food, but the proportion in the blood is constant. This is another fact in favor of the view that the presence of a definite quantity of common salt in the circulating fluid is essential to the proper performance of the general function of nutrition.

Origin and Discharge of Chloride of Sodium.—This substance is always introduced with food in the condition in which it is found in the body. It is contained in the substance of all kinds of food, animal and vegetable; but, in the herbivora and in man, this source is not sufficient to supply the wants of the system, and it is introduced, therefore, as salt. The quantity which is discharged from the body has been estimated by Barral to be somewhat less than the quantity introduced, about one-fifth disappearing; but these estimates are not exactly accurate, for the amount thrown off in the perspiration has never been directly ascertained. It exists in the blood in connection with the phosphate of potassa, and a certain amount is lost in a double decomposition which takes place between these two salts, resulting in the formation of chloride of potassium and phosphate of soda. It also is supposed to furnish the soda to all the salts which have a soda base, and a certain quantity, therefore, disappears in this way.

Existing, as it does, in all the solids and fluids of the body, chloride of sodium is discharged in all the excretions, being thrown off in the urine, fæces, perspiration, and mucus.

Chloride of Potassium.—Chloride of potassium, although neither so important a proximate principle as the chloride of sodium nor so generally distributed in the economy, seems to have an analogous function. It is found in the muscles, liver, milk, chyle, blood, mucus, saliva, bile, gastric juice, cephalo-rachidian fluid, and urine. It is exceedingly soluble, and in these situations it exists in solution in the fluids. Its quantity in these situations has not been accurately ascertained, as it has generally been estimated in connection with the chloride of sodium. In the muscles, it exists, however, in a larger proportion than common salt. In cow's milk, Berzelius has found 1·7 part per 1,000; Pfaff and Schwartz, 1·35 per 1,000 in cow's milk, and 0·3 per 1,000 in human milk. Of the function of this principle, little remains to be said after what has been stated with regard to the chloride of sodium. The functions of these two principles are probably identical, although the latter, from its greater quantity in the fluids and its universal distribution, is by far the more important.

Origin and Discharge of Chloride of Potassium.—This substance has two sources; one in the food, existing, as it does, in muscular tissue, milk, etc., and the other in a chemical reaction between the phosphate of potassa and the chloride of sodium, forming the chloride of potassium and the phosphate of soda. That this decomposition takes place in the body, is evident from the fact that the ingestion of a considerable quantity of common salt has been found, in the sheep, to increase the quantity of chloride of potassium in the urine, without having any influence upon the amount of chloride of sodium. The chloride of potassium is discharged from the body in the urine and mucus.

Phosphate of Lime.—This salt is found in all the solids and fluids of the body. As it is always united, in the solids, with organic substances as an important element of constitution, it is hardly second in importance to water. It differs in its functions so essentially from the chlorides of sodium and potassium, that they are hardly to be compared. It is insoluble in water, but is held in solution in the fluids of the body by virtue of free carbonic acid, the bicarbonates, and the chloride of sodium. In the solids and semi-solids, the condition of its existence is the same as that of water; *i. e.* it is incorporated, particle to particle, with the organic substance characteristic of the tissue and is one of its essential elements of composition, and cannot be completely separated without incineration. Nothing need be added here with regard to this mode of union in the body of organic and inorganic substances, after what has been said under the head of water.

The following table gives the relative quantities of phosphate of lime in various situations:

Table of Quantities of Phosphate of Lime.

	Parts per 1,000.
In Arterial blood, } Poggiale and Marchal	0·79
" Venous blood, } Poggiale and Marchal	0·76
" Milk, human (Pfaff and Schwartz)	2·50
" Saliva (Wright)	0·60
" Urine, proportion to weight of ash (Fleitmann)	25·70
" Excrements (Berzelius)	40·00
" Bone (Lassaigne)	400·00
" Vertebra of a rachitic patient (Bostock)	136·00
" Teeth of an infant one day old } Lassaigne	510·00
" Teeth of adult } Lassaigne	610·00
" Teeth, at eighty-one years } Lassaigne	660·00
" Enamel of the teeth } Lassaigne	885·00

By this table it is seen that the phosphate of lime exists in very small quantity in the fluids but is abundant in the solids. In the latter, the quantity is in proportion to the hardness of the structure, the quantity in enamel being, for example, more than twice that in bone. The variations in quantity with age are very considerable. In the teeth of an infant one day old, Lassaigne found 510 parts per 1,000; in the teeth of an adult, 610 parts; and in the teeth of an old man of eighty-one years, 660 parts. This increase in the calcareous elements of the bones, teeth, etc., in old age is very marked; and in extreme old age they are deposited in considerable quantity in situations where there existed but a small proportion in adult life. The system seems to gradually lose the property of appropriating to itself organic matters; and, although articles of food are digested as well as ever, the power of assimilation by the tissues is diminished. The bones become brittle, and fractures, therefore, are common at this period of life, when dislocations are almost unknown. Inasmuch as the real efficiency of organs depends upon organic matters, the system actually wears out, and this progressive change finally unfits the various parts for the performance of their functions. An individual, if he escape accidents and die, as we term it, of old age, passes away thus by a simple wearing out of his organism.

Function of Phosphate of Lime.—This substance, as before remarked, enters largely into the constitution of the solids of the body. In the bones its function is most apparent. Its existence, in suitable proportion, is necessary to the mechanical office of these parts, giving them their power of resistance, without rendering them too brittle. It is more abundant in the bones of the lower extremities, which have to sustain the weight of the body, than in those of the upper extremities; and in the ribs, which are elastic rather than resisting, it exists in less quantity than in the bones of the arm.

The necessity of a proper proportion of phosphate of lime in the bones is made evident by cases of disease. In rachitis, where, as is seen by the table, its quantity is very much diminished, the bones are unable to sustain the weight of the body, and they become deformed; and finally, when the phosphate of lime is deposited, they retain their distorted shape. The phosphate of lime may be extracted from the bones by maceration in dilute hydrochloric acid, which dissolves it, leaving only the organic substance. Bones treated in this way, although they retain their form, become very pliable; and a long slender bone, like the fibula, may be actually tied into a knot.

Origin and Discharge of Phosphate of Lime.—The origin of this principle is exclusively from the external world. It enters into the constitution of our food and is discharged in the fæces, urine, and other matters thrown off by the body. Its quantity in the urine is exceedingly variable. Lecanu found from 0·437 to 29·250 grains thrown off by the kidneys during the twenty-four hours.

Carbonate of Lime.—This principle exists in the bones, teeth, cartilage, internal ear, blood, sebaceous matter, and sometimes in the urine. It exists as a normal constituent in the urine of some herbivora, but not in the carnivora or in man. It is most appropriately considered immediately after the phosphate of lime, because it is the salt next in importance in the constitution of the bones and teeth. In these structures it exists intimately combined with the organic matter, under the same conditions as the phosphates, and it has analogous functions. In the fluids it exists in small quantity and is held in solution by virtue of free carbonic acid and the chloride of potassium.

The carbonate of lime is the only example of an inorganic proximate principle existing uncombined and in a crystalline form in the body. In the internal ear it is found in this form and has some function connected with audition.

Table of Quantities of Carbonate of Lime.

		Parts per 1,000.
In Bone, human (Berzelius)		113·00
" " " (Marchand)		102·00
" " " (Lassaigne)		76·00
" Teeth of an infant one day old	Lassaigne	140·00
" Teeth of an adult	Lassaigne	100·00
" Teeth of an old man, eighty-one years	Lassaigne	10·00
" Urine of the horse (Boussingault)		10·82

Origin and Discharge of Carbonate of Lime.—Carbonate of lime is introduced into the body with our food, held in solution in water by the carbonic acid which is always present in small quantity. It is also formed in the body, particularly in the herbivora, by a decomposition of the tartrates, malates, citrates, and acetates of lime contained in the food. These salts, meeting with carbonic acid, are decomposed, and the carbonate of lime is formed. It is probable that, in the human subject, some of it is changed into the phosphate of lime, and in this form is discharged in the urine; but when and how this change takes place has not been definitely ascertained.

Carbonate of Soda.—This salt is found in the blood and saliva, giving to these fluids their alkalinity; in the urine of the human subject, when it is alkaline without being ammoniacal; in the urine of the herbivora; and in the lymph, cephalo-rachidian fluid, and in bone. The analyses of chemists with regard to this substance are very contradictory, on account of its formation during the process of incineration; but there is no doubt that it is found in the above situations. The following table gives the quantities which have been found in some of the fluids and solids:

Table of Quantities of Carbonate of Soda.

	Parts per 1,000.
In Blood of the ox (Marcet)	1·62
" Lymph (Nasse)	0·56
" Cephalo-rachidian fluid (Lassaigne)	0·60
" Compact tissue of the tibia in a male of 38 years (Valentin)	2·00
" Spongy tissue of the same (Valentin)	0·70

Function of Carbonate of Soda.—This substance has a tendency to maintain the fluidity of the albuminoid constituents of the blood, and it assists in preserving the form and consistence of the blood-corpuscles. Its function in nutrition is rather accessory, like that of chloride of sodium, than essential, like the phosphate of lime, in the constitution of certain structures.

Origin and Discharge of Carbonate of Soda.—This substance is not introduced into the body as carbonate of soda, but it is formed, as is the carbonate of lime in part, by a decomposition of the malates, tartrates, etc., which exist in fruits. It is discharged occasionally in the urine of the human subject, and a great part of it is decomposed in the lungs by the action of pneumic acid, setting free carbonic acid, which is discharged in the expired air.

Carbonate of Potassa.—This salt exists particularly in herbivorous animals. It is found in the human subject when subjected to a vegetable diet. Under the heads of function, origin, and discharge, what has been said with regard to the carbonate of soda will apply to the carbonate of potassa.

Carbonate of Magnesia and Bicarbonate of Soda.—It is most convenient to take up these two salts in connection with the other carbonates, though they are put at the end of the list of inorganic substances as the least important. We know very little about them, chemically or physiologically. Traces of carbonate of magnesia have been found in the blood of man, and it exists normally in considerable quantity in the urine of herbivora. In the human subject it is discharged in the sebaceous matter.

Liebig has merely indicated the presence of bicarbonate of soda in the blood.

Phosphate of Magnesia, Phosphate of Soda (neutral), and Phosphate of Potassa.—These salts are found in all the fluids and solids of the body, though not existing in a very large proportion, as compared with the phosphate of lime, which we have already considered. In their relations to organized structures, they are analogous to the phosphate of lime, entering into the composition of the tissues, and existing there in a state of intimate combination. They are all taken into the body with food, especially by the carnivora, in the fluids of which they are found in much greater abundance than the carbonates; which latter, as we have already seen, are in great part the result of the decomposition by carbonic acid of the malates, tartrates, oxalates, etc. With respect to their functions, we can only say that, with the phosphate of lime, they go to form the organized structures of which they are necessary constituents. They are discharged from the body in the urine and fæces.

Sulphate of Soda, Sulphate of Potassa, and Sulphate of Lime.—The sulphate of soda and the sulphate of potassa are identical in their situation, and apparently in their functions. They are found in all the fluids and solids of the body, except in the milk, bile, and gastric juice. Their origin in the body is from the food, in which they are contained in small quantity, and they are discharged in the urine. Their chief function appears to be in the blood, where they tend to preserve the fluidity of the albuminoid matters and the form and consistence of the blood-corpuscles. The sulphate of lime is found in the blood and fæces. It is introduced into the body in solution in the water which is used as drink, and it is discharged in the fæces. Its function is not understood and is probably not very important.

Hydrochlorate of Ammonia.—This substance has simply been indicated by chemists as existing in the gastric juice of ruminants, the saliva, tears, and urine. Some chemists make a rearrangement of its atoms, calling it chloride of ammonium. It is discharged in the urine, in which it exists, according to Simon, in the proportion of 0·41 part per 1,000. Its origin and function are unknown. Various combinations of bases with organic acids taken as food, as the acetates, tartrates, etc., found in fruits, undergo decomposition in the body and are transformed into carbonates. In this form they behave precisely like the other inorganic salts.

Principles consumed by the Organism.

All of the assimilable organic matter taken as food is consumed in the organism, and none is ever discharged from the body, in health, in the form under which it was introduced. The principles thus consumed in nutrition have been divided into nitrogenized and non-nitrogenized; and, although they both disappear in the organism, they possess certain marked differences in their properties, and probably, also, in their relations to nutrition.

Nitrogenized Principles.—The nitrogenized principles, having for their basis, carbon, hydrogen, nitrogen, and oxygen, undergo, in the process of digestion and absorption, remarkable changes; but these are more marked as regards their properties than their ultimate chemical composition. They are all converted into the nitrogenized elements of the blood, which, in their turn, are transformed into the characteristic nitrogenized principles of the different tissues, and are appropriated by these tissues, to supply the place of worn-out matter. With the intimate nature of this series of transformations, we are entirely unacquainted; but we know that the deposition of new nitrogenized matter in the tissues, constituting one of the most important of the acts of nutrition, is attended with a corresponding loss of matter that has become changed into the nitrogenized elements of excretion. It is the intermediate series of phenomena that is so obscure.

The nutrition of the nitrogenized elements of the tissues may be greatly modified by the supply of new matter. For example, a diet composed of nitrogenized matter in a readily assimilable form will undoubtedly affect favorably the development of the corresponding tissues of the body; and, on the other hand, a deficiency in the supply will produce a corresponding diminution in power and development. The modifications in nutrition due to supply have, however, certain well-defined limits. An excess taken as food is not discharged in the fæces, nor does it pass out in the form in which it entered, in the urine; but it apparently undergoes digestion, becomes absorbed by the blood, and increases the quantity of nitrogenized excrementitious matter discharged, particularly the urea. This fact is shown by the great increase in the elimination of urea produced by an excess of nitrogenized food. Whether the nitrogenized matter that is not actually needed in nutrition be changed into urea in the blood, or whether it be appropriated by the tissues, increasing the activity of their disassimilation, is a question difficult to determine experimentally. Certain it is, however, that an excess of nitrogenized food is thrown off in nearly the same way as an excess of inorganic matter; the difference being that the latter passes out in the form in which it has entered, and the former is discharged in the form of nitrogenized excrementitious matter.

Development of Power and Endurance by Exercise and Diet (*Training*).—The nutrition of the nitrogenized elements of the body is greatly influenced by functional exercise. This is partly local and partly general in its effects. For example, by the persistent exercise of particular muscles, their development can be carried to a high degree of perfection, the rest of the muscular system undergoing no change; or the entire muscular system may, by appropriate general exercise, be made to increase considerably in volume, and a person may become capable of great endurance, under an ordinary diet. It is surprising, sometimes, to see how small an amount of well-regulated exercise will accomplish this end. But, if it be desired to attain the maximum of strength and endurance, it is necessary to carefully regulate the diet as well as the exercise. Those who are in the habit of "training" men, particularly for pugilistic encounters, have long-since demonstrated practically certain facts which physiologists have been rather slow to appreciate. By carefully regulating the diet, confining it chiefly to nitrogenized articles, eliminating fat entirely, and reducing the starchy elements to the minimum; by regulating the exercise so as to increase the nutritive activity of all the muscles to the greatest possible extent; by increasing the respiratory activity by running, etc., and removing from the body all the unnecessary adipose tissue; by all these means, which favor nutritive assimilation by the nitrogenized elements of the organism, a man may be "trained" so as to be capable of immense muscular effort and endurance.

The process of training, skilfully carried out, is in accordance with what are now admitted as physiological laws; although it has been practised for years by ignorant persons, and its rules are entirely empirical. It is stated that the athletes of ancient times, while vigorously exercising the muscles, favored by their diet the development of fat, so as to be better able to resist the blows of their antagonists. However this may be, since the English prize-ring has been regularly organized, or since about the middle of the last century, the system of training has been entirely different, and fat has been, as far as possible, removed from every part of the body. Fat is regarded by trainers as inert matter; and they recognize, practically at least, the fact that the characteristic functions of parts depend for their activity upon their nitrogenized constituents. The contraction of a muscle, for example, is powerful in proportion to the amount and condition of its musculine; and it has been ascertained by experience that the muscular system can be most thoroughly developed by carefully-graduated exercise and a diet composed largely of nitrogenized matter. In the regular system of training, starch, sugar, fat, and liquids are avoided; and the diet is confined almost entirely to rare meats, eggs, and stale bread or toast, with oatmeal-gruel. The oatmeal has been used from time immemorial, and it is supposed to be useful in keeping the bowels in good condition. A very small amount of alcohol and of other nervous stimulants, chiefly in the form of home-brewed ale, sherry wine, and tea, is allowed. Sexual intercourse and all unusual nervous excitement are interdicted.

Those who adopt absolutely the classification of food into plastic, or tissue-forming, and calorific, or respiratory, would regard this course of diet as eminently plastic; but, during the severe habitual exercise, which is most rigid after the man has been "trained down" so that his fat is reduced to the minimum, the respiratory power and the exhalation of carbonic acid are immensely increased, while the proportion of hydro-carbons in the food is very small.

We do not propose to discuss from a scientific point of view all of the minutiæ of training. Many of its traditional rules are trivial and unimportant; but it is certainly a question of great physiological interest to study the processes by which the muscular strength and endurance of a man may be brought to the highest possible point of development.

One of the most remarkable of the results of thorough training is the development of immense endurance and "wind." This is accomplished by running and prolonged exercise, not so violent as to be exhausting, and always followed by ablutions and frictions, so as to secure a full reaction. The surprising faculty of endurance thus developed must be due in a great measure to nervous power as well as to a gradual, careful, and perfectly physiological development of the muscular system. A man may be brought into the ring in what would appear to be perfect condition; but, if he be trained down too much or too rapidly, he is liable to give out after comparatively slight exertion. A man who does not possess the required constitutional stamina and nervous power is likely to break down in training, and he cannot be brought to proper condition. On the other hand, a man in perfect condition is capable of the maximum of muscular exertion for an hour, or can easily walk a hundred miles in a day.

It is a question of great importance, in connection with the subject of nutrition, to determine whether the extraordinary muscular power developed by severe training be, in the end, beneficial or deleterious. This can be answered very easily upon practical as well as theoretical grounds. A fully-grown, well-developed man, in perfect health, may be trained so as to be brought to what is technically called fine condition, and he will present at that time all the animal functions in their perfection. He is then a model of a physical man; and the only consequences that can result from such a course are beneficial. The argument that professional pugilists are short-lived is fallacious; for it is well known that almost all of them, after training for and passing through an encounter, immediately relapse into a course of life in which all physiological laws are habitually violated.

During training, even of the most severe character, not only is great attention paid to diet and exercise, but all of the functions are scrupulously watched. Tranquillity of mind, avoidance of exhaustion, of artificial excitement, stimulants, tobacco, etc., are strictly enjoined; and the process is always very gradual, especially at its commencement, and is continued for several months. The cases in which training has been followed by bad effects are entirely different. Undeveloped boys are frequently trained for boating, in the most reckless manner, until they break down. An attempt is made to accomplish in a few weeks what can only be done physiologically in several months; and the result is, that some of the vital organs, particularly the heart, are liable to become permanently injured. To improve the "wind" and endurance, a person undergoes the most violent exercise, which is followed by great exhaustion, intense respiratory distress, and disturbance of the action of the heart, these parts being suddenly forced far beyond their functional capacity. This cannot be done without danger of permanent disturbances of the system, such as have been frequently observed; and it is all the more liable to be followed by bad results, from the fact that amateurs are trained together, five or six under one man, and are more or less independent, while the professional athlete is never out of the sight of his trainer for months, and during that time is under complete control. There is, it seems, every physiological reason to believe that it is beneficial to the general system to bring it to the highest point of functional activity by training; but, if this be not done with great caution and judgment, it is liable to be followed by serious results.

Non-Nitrogenized Principles.—The non-nitrogenized principles present a marked contrast to the alimentary substances we have just considered. In the first place, they are not indispensable to the nutrition of all animals. The carnivora, for example, may be well nourished upon a diet composed exclusively of nitrogenized matter; and the remarks we have just made upon training show that the human subject may be brought to a high condition of physical development, when starch, sugar, and fat are almost entirely eliminated from the food. This shows conclusively that the division of the food into plastic and calorific elements is not absolute, and that the animal temperature may be maintained without the hydro-carbons. The nitrogenized principles are probably the only class of alimentary substances capable of forming muscular tissue; but, by certain transformations, with the exact nature of which we are imperfectly acquainted, this class of substances is capable of producing heat and of furnishing the carbonic acid eliminated in respiration. The non-nitrogenized principles are incapable in themselves of meeting the nutritive demands of the system, and they are either consumed without forming part of the tissues or are deposited in the form of fat. These questions we have already considered under the head of alimentation; and it will be remembered that, with a few exceptions, fat always exists in the body uncombined, either in the form of adipose tissue or of fatty granulations in the substance of other tissues.

The non-nitrogenized elements taken up by the blood may be divided into two varieties: one, the sugars, composed of carbon with hydrogen and oxygen in the proportions to form water, constituting the true hydro-carbons; and the other, the fats, in which the hydrogen and oxygen do not exist in the proportion to form water. We speak of the sugars only, because starch and all varieties of sugar taken as food are transformed into glucose.

In connection with the study of alimentation and glycogenesis, we have already referred to the destination of the true hydro-carbons in the organism. They are taken as food to a considerable extent, particularly in the form of starch, and are formed constantly by the liver in all classes of animals. Sugar is never discharged from the body in health, nor is it deposited in any part of the organism, even as a temporary condition. It generally disappears in the passage of the blood through the lungs. In studying the changes which sugar is capable of undergoing, it has been found that it may be converted into lactic acid or be changed into carbonic acid and water; but precisely to what extent the sugars undergo these changes, or how they are acted upon by the inspired oxygen, it has been impossible thus far to determine. We must be content to say that the exact changes which the sugars undergo in nutrition are unknown. They seem to be very important in development, being abundant in the food and formed largely in the system in early life. They certainly do not enter into the composition of the tissues; and it would seem that they must be important in the two remaining phenomena of nutrition, namely, the formation of fat and the development of animal heat. The relations of sugar to these two processes will be taken up under their appropriate heads.

The fats taken as food are either consumed in the organism or are deposited in the form of adipose tissue. That the fats are consumed, there can be no doubt; for, in the normal alimentation of man, fat is a constant article, and it is never discharged from the body. We are forced to admit, however, that the changes which fat undergoes in its process of destruction are not thoroughly understood. All that we positively know is, that the fatty principles of the food are formed into a fine emulsion in the small intestine, and are taken up, chiefly by the lacteals, and discharged into the venous system. For a time, during absorption, fat may exist in certain quantity in the blood; but it soon disappears and is either destroyed directly in the circulatory system or is deposited in the form of adipose tissue to supply a certain amount of this substance consumed. That it may be destroyed directly is proven by the consumption of fat in instances where the amount of adipose matter is insignificant; and that the adipose tissue of the organism may be consumed is shown by its rapid disappearance in starvation.

The question of the relations of fat to nutrition is important but somewhat obscure. It does not take part in the nutrition of the parts that are endowed to an eminent degree with the so-called vital functions; and, when these tissues are brought to their highest point of development, the fat is entirely removed from their substance. If fat be not a plastic material, it would seem to have no function remaining but that of keeping up, by its oxidation, the animal temperature. But it is not proven that the fats, or fats and sugar, are the sole principles concerned in the production of carbonic acid and the generation of heat; for both of these phenomena occur in the carnivora, and in man, when fat and sugar are eliminated from the food and the fat in the body has been reduced to the minimum. Fat is undoubtedly destroyed in the organism, and probably it assists in the formation of the carbonic acid eliminated; it is also taken in much larger proportion in cold than in temperate or warm climates; but we cannot, with our present information, say without reserve that fats and sugar are oxidized directly, by a process with which we are familiar under the name of combustion, and that their exclusive function is the production of animal heat.

It is a curious fact that fat is generally deposited in tissues during their retrograde processes. The muscular fibres of the uterus, during the involution of this organ after parturition, become the seat of a deposit of fatty granulations. Long disuse of any part will produce such changes in its power of appropriating nitrogenized matter for its regeneration, that it soon becomes atrophied and altered. Instead of the normal nitrogenized elements of the tissue, we have, under these circumstances, a deposition of fatty matter. The fat is here inert, and it takes the place of the substance that gives to the part its characteristic functions. These phenomena are strikingly apparent in muscles that have been long disused or paralyzed and in nerves that have lost their functional activity. If the change be not too extensive, the fat may be made to disappear, and the part will return to its normal constitution, with appropriate exercise; but frequently the alteration has proceeded so far as to be irremediable and permanent.

Accurate observations have shown that, in young animals rapidly fattened, all the adipose matter in the body cannot be accounted for by what is taken in as food; and it is certain that fat may be produced *de novo* in the organism.

Formation and Deposition of Fat.—The question of the generation of fat in the economy is one of great importance. Whatever the exact nature of the changes accompanying the destruction of non-nitrogenized matters may be, it is certain that the fat stored up in the body is consumed, when there is a deficiency in any of the elements of food, as well as that which is taken into the alimentary canal. It is rendered probable, indeed, by the few experiments that have been made upon the subject, that obesity increases the power of resistance to inanition. At all events, in starvation, the fatty constituents of the body are the first to be consumed, and they almost entirely disappear before death. As we have already seen, sugar is never deposited in any part of the organism, and it is merely a temporary constituent of the blood. If the sugars and fats have, in certain regards, similar functions in nutrition, and if, in addition to the mechanical functions of fat, it may be retained in the organism for use under extraordinary conditions, it becomes very important to ascertain the mechanism of its production and deposition.

The production of fatty matter by certain insects, in excess of the fat supplied with the food, was established long ago by the researches of Huber; and analogous observations have been made upon birds and mammals by Boussingault. Some of the experiments of Boussingault are peculiarly interesting, as they were made upon pigs, in which the digestive apparatus closely resembles that of the human subject. They showed conclusively that, under certain circumstances, more fat exists in the bodies of animals than can be accounted for by the total amount of fat taken as food added to the fat existing at birth. In some very interesting experiments with reference to the influence of different kinds of food upon the development of fat, it was ascertained that fat could be produced in animals upon a regimen, sufficiently nitrogenized, but deprived of fatty matters; but the fact should be recognized that "the nutriment which produces the most rapid and pronounced fattening is precisely that which joins to the proper proportion of albuminoid substances the greatest proportion of fatty principles."

Animals cannot be fattened without a certain variety in the regimen. We have already discussed the necessity of a varied diet and have shown that an animal will die of starvation when confined exclusively to one class of principles, even if this be of the most nutritious character; and it is not necessary to refer again to the experiments which have demonstrated that a diet confined exclusively to starch, sugar, or fat, or even pure albumen or fibrin, cannot sustain life, much less fatten an animal. We are prepared, then, to understand why, in the pigs experimented upon by Boussingault, a regimen confined to potatoes did not prove to be fattening, notwithstanding the large proportion of starch, and that fat was produced in abundance only when the food presented the proper variety of principles.

Very little is known concerning the precise mechanism of the production of fat. The experiments of Boussingault seem to leave no doubt that it may be formed from any kind of food, even when the alimentation is exclusively nitrogenized; but it is, nevertheless, a matter of common observation that certain articles of diet are more favorable to its deposition than others; and it is also true that the herbivora are fattened much more readily, as a rule, than the carnivora.

Theoretical considerations would immediately point to starch and sugar as the elements of food most easily convertible into fat, as they contain the same elements, though in different proportions; and it is more than probable that this view is correct. It is said that, in sugar-growing sections, during the period of grinding the cane, the laborers become excessively fat, from eating large quantities of the saccharine matter. We cannot refer to any exact scientific observations upon this point, but the fact is pretty generally admitted by physiologists. Again, it has been frequently a matter of individual experience that sugar and starch are favorable to the deposition of fat, especially when there is a constitutional tendency to obesity. A most remarkable example of this, and one which has met with considerable notoriety, is worthy of mention, though not reported by a scientific observer. We refer to the letter on corpulence, by Mr. Banting. The writer of this curious pamphlet, in 1862, was sixty-six years old, five feet and five inches in height, and weighed two hundred and two pounds. Under the advice of Mr. William

Harvey, F. R. C. S., of London, he confined himself to a diet containing no sugar and as little starch and fat as possible. Continuing this regimen for one year, he gradually lost weight, at the rate of about one pound each week, until he was reduced to one hundred and fifty-six pounds. At the time the last edition of the pamphlet was published, in 1864, he enjoyed perfect health and weighed one hundred and fifty pounds, his weight varying only to the extent of one pound, more or less, in the course of a month. This little tract is very interesting, both from the importance of its physiological deductions and its quaint literary style. It has had an immense circulation, and many persons suffering from excessive adipose development have adopted the system here advised, with results more or less favorable. A study of the course of diet here prescribed shows it to be a pretty rigid training system, with the exception of succulent vegetables and liquids, which are allowed without restriction. It is proper to remark, however, that some enthusiastic advocates of the plan have exceeded the limits prescribed and have neglected the caution of the author always to employ it under the advice of a physician; and its too rigid enforcement has been followed by serious disturbances in general nutrition. Others, however, have verified the favorable results obtained by Mr. Banting.

It is difficult to explain the remarkable constitutional tendency to obesity observed in some individuals, which is very often hereditary. Such persons will become very fat upon a comparatively low diet, while others deposit but little adipose matter, even when the regimen is abundant. It is to be noted, however, that the former are generally addicted to the use of starchy, saccharine, and fatty elements of food, while the latter consume a greater proportion of nitrogenized matter.

It is not an uncommon remark that the habit of taking large quantities of liquids favors the formation of fat; but it is not easy to find any scientific basis for such an opinion. As to the formation of fat by any particular organ or organs in the body, no positive scientific view has been advanced, except the proposition by Bernard, that the liver had this function, in addition to its glycogenic office. This we have already discussed and have shown that such a function is far from being positively established.

Condition under which Fat exists in the Organism.—It is said that fat combined with phosphorus is united with nitrogenized matter in the substance of the nervous tissue; but its condition here is not well understood, as we shall see when we come to treat of the nervous system. A small quantity of fat is contained in the blood-corpuscles, and a little is held in solution in the bile; but, with these exceptions, fat always exists in the body isolated and uncombined with nitrogenized matter, in the form of granules or globules and of adipose tissue. The three varieties of fat are here combined in variable proportions, which is the cause of the differences in its consistence in different situations. The ultimate elements of fat are, carbon, hydrogen, and oxygen, the two latter in unequal proportions.

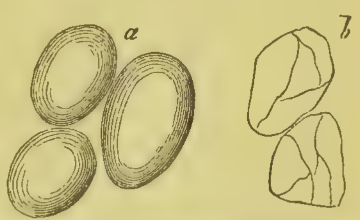


FIG. 145.—*Adipose vesicles; magnified 350 diameters.* (Kölliker.)

a, normal adipose vesicles from the breast; *b*, vesicles treated with ether, by which the fat is dissolved, the empty vesicles remaining.

Physiological Anatomy of Adipose Tissue.—Adipose tissue is found in abundance in the interstices of the subcutaneous areolar tissue, where it is sometimes known as the panniculus adiposus. It is not, however, to be confounded with the so-called cellular or areolar tissue, and is simply associated with it without being one of its essential parts; for the areolar tissue is abundant in certain situations, as the eyelids and scrotum, where there is no adipose matter, and adipose tissue exists sometimes, as in the marrow of the bones, without any areolar tissue.

Adipose tissue is widely distributed in the body and has important mechanical functions. Its anatomical element is a vesicle, from $\frac{1}{800}$ to $\frac{1}{300}$ of an inch in diameter, composed of a delicate, structureless membrane, $\frac{1}{25000}$ of an inch thick, enclosing fluid contents. The form of the vesicles is naturally rounded or ovoid; but in microscopical preparations they are generally compressed so as to become irregularly polyhedrical. The membrane sometimes presents a small nucleus attached to its inner surface. The contents are, a minute quantity of an albuminoid fluid moistening the internal surface of the membrane, and a mixture of oleine, margarine, and stearine, liquid at the temperature of the body, but becoming harder on cooling. Little rosettes formed of acicular crystals of margarine are frequently observed in the fat-vesicles, when the temperature is rather low.

The adipose vesicles are collected into little lobules, from $\frac{1}{25}$ to $\frac{1}{4}$ of an inch in diameter, which are surrounded by a rather wide net-work of capillary blood-vessels. Close examination of these vessels shows that they frequently surround individual fat-cells, in the form of single loops. There is no distribution of nerves or lymphatics to the elements of adipose tissue. It is seen by this sketch of the structure of adipose tissue, that there is no anatomical reason for classing these vesicles with the ductless glands, as is done by some physiologists. They undoubtedly, under certain conditions, have the power of filling themselves with fat; but it would be no more appropriate to call fat a secretion than to apply this term to the development and nutrition of the muscular substance within the sarcolemma.

Conditions which influence Nutrition.—We know more concerning the conditions that influence the general process of nutrition than about the nature of the process itself. It will be seen, for example, when we come to study the nervous system, that there are nerves which regulate, to a certain extent, the nutritive forces. We do not mean to imply that nutrition is effected through the influence of the nerves, but it is the fact that certain nerves, by regulating the supply of blood, and perhaps by other influences, are capable of modifying the nutrition of parts to a very considerable extent.

In discussing the influence of exercise upon the development of parts, we have shown that this is not only desirable but indispensable; and the proper performance of the functions of nearly all parts involves the action of the nervous system. It is true that the separate parts of the organism and the organism as a whole have a limited existence; but it is not true that the change of nitrogenized, living substance into effete matter, a process that is increased in activity by physiological exercise, consumes, so to speak, a definite amount of the limited life of the parts. Physiological exercise increases disassimilation, but it also increases the activity of nutrition and favors development. It is a favorite sophism to assert that bodily or mental effort is made always at the expense of a definite amount of vitality and matter consumed. This is partly true, but mainly false. Work involves change into effete matter; but, when restricted within physiological limits, it engenders a corresponding activity of nutrition, assuming, of course, that the supply from without be sufficient. Other things being equal, a man will live longer under a system of physiological exercise of every part, than if he made the least effort possible. It is, indeed, only by such use of parts that they can undergo proper development and become the seat of normal nutrition. But, notwithstanding all these facts, life is self-limited. Unless subjected to some process which arrests all changes, such as cold, the action of preservative fluids, etc., organic substances are constantly undergoing transformation. In the living body, their disassimilation and nutrition are unceasing; and, after they are removed from what are termed vital conditions, they change, first losing irritability, or becoming incapable of performing their functions, and afterward decomposing into matters which, like the results of their disassimilation, are destined to be appropriated by the vegetable kingdom. Nutrition sufficient to supply the physiological decay of parts cannot continue indefinitely. The wonderful forces in the fecundated ovum lead it through a process of development that requires, in the human subject, more than twenty years for its completion; and, when development ceases, no one can say why it becomes arrested, nor can we give any sufficient reason why, with a sufficient and appropriate supply of material, a man should not grow indefinitely. After the being is fully developed, and during what is known as the adult period, the supply seems to be about equal to the waste. But, after this, nutrition gradually becomes deficient, and the deposition of new matter in progressive old age becomes more and more inadequate to supply the place of the living nitrogenized substance. We may at this time, as an exception, have a considerable deposition of fat, but the nitrogenized matter is always deficient, and the proportion of inert, inorganic matter combined with it is increased.

There can be little if any doubt that the forces which induce the regeneration or nutrition of parts reside in the organic nitrogenized substance, and that these give to the parts their characteristic functions, which we call vital; the inorganic matter being passive, or having, at the most, purely physical functions. If, therefore, as age advances, the organic matter be gradually losing the power of completely regenerating its substance, and if its proportion be progressively diminishing while the inorganic matter is increasing in quantity, a time will come when some of the organs necessary to life will be unable to perform their office. When this occurs we have death from old age, or physiological dissolution. This may be a gradual failure of the general process of nutrition, or it may attack some one organ or system. Why death is thus certain to occur, we do not know, any more than we can explain why and how animals live.

The modifications in nutrition due to the very varied influences that may be brought to bear upon it present a most extended subject for discussion; but we shall not touch upon any of these influences that are not purely physiological. Among the most interesting of these modifications, are those due to age, constituting, as they do, in early life, the process of development. These will be treated of fully in connection with the subject of generation. It is evident, also, from what we have already said, that each tissue and organ has its own conditions of nutrition and development; and this constitutes another important division of the subject, the more interesting, because the nutrition and development of the individual tissues are closely connected with the processes of regeneration and repair after injury. We have stated, as far as possible, all that is positively known of the nutrition of the fully-formed tissues of the body; but the history of their development belongs to embryology. If we were to attempt to follow the processes of regeneration after injury, in nerves, muscles, bone, etc., we should be compelled to pass almost immediately into the domain of pathology. The influences of climate, respiratory activity, food, etc., have already been considered under the heads of respiration, alimentation, and excretion, and will be touched upon again in connection with animal heat.

Products of Disassimilation.—It only remains now to recapitulate briefly the mode of production of the excretions. The process of disassimilation, we are aware, always accompanies nutrition, and the substances thus formed are the result of the final changes of the organic constituents of the tissues. As we have seen in studying the urine, the excrementitious principles proper are always associated with inorganic matter which has passed through the organism; and, while there are many effete substances that we have been able to recognize, the physiological and pathological relations of which have been more or less successfully studied, there are probably others which have thus far escaped observation. It is almost futile to speculate upon the probable bearing which the discovery of new excrementitious principles will have upon pathological conditions, while there are so many which we now know only by name, their relations to the different tissues being still obscure; but, if we reason from the light thrown upon certain diseased conditions by the fact that urea, the urates, and cholesterine are liable to be retained in the blood and produce certain symptoms, we may safely infer that the description of new effete principles will have an important influence upon our pathological knowledge as well as our comprehension of physiological processes. The following are the most important excrementitious matters, the relations of which to nutrition and disassimilation are more or less fully understood:

Products of Disassimilation.

Excrementitious Principles.	*How excreted.*
Carbonic acid	Principally by the lungs; but also by the skin, and in solution in the excreted fluids.
Alkaline sudorates	Perspiration.
Urea	Principally in the urine; but a certain quantity in the perspiration.
Urate of soda	Urine.
Urate of ammonia	"
Urate of potassa	"
Urate of lime	"
Urate of magnesia	"
Hippurate of soda	"
Hippurate of potassa	"
Hippurate of lime	"
Creatine	"
Creatinine	"
Oxalate of lime	"
Xanthine	"
Stercorine (changed from cholesterine)	Fæces.
Excretine	"

In the above list we have omitted all doubtful excrementitious principles, as well as the inorganic compounds found in the excreted fluids; and we may assume that the substances therein enumerated represent, as far as we are now able to determine, the physiological wear of the organism. We shall not again discuss the fact that the life of tissues involves physiological waste or decay, and that the excrementitious principles proper represent the final changes of organic substances. We know that this process goes on without necessarily involving exercise of the peculiar functions of the parts; but it is no less true that exercise, or work, increases the activity both of nutrition and wear. This is one of the great principles underlying all our ideas of the process of nutrition. We shall not discuss here the influence of work upon the elimination of some of the nitrogenized compounds, particularly urea, for we have already examined that subject most carefully in another place; but we have no hesitation in stating, as a general law that has yet to meet with exceptions, that physiological work increases excretion.

Animal Heat.

The process of nutrition in animals is always attended with the development of heat, and it produces a temperature more or less independent of external conditions. This is true in the lowest as well as the highest animal organizations; and analogous phenomena have even been observed in plants. In cold-blooded animals, nutrition may be suspended by a diminished external temperature, and certain of the functions become temporarily arrested, to be resumed when the animal is exposed to a greater heat. This is true, to some extent, in certain warm-blooded animals that periodically pass into a condition of stupor, called hibernation; but in man, and in nearly all the warm-blooded animals, the general temperature of the body can undergo but slight variations. The animal heat is essentially the same in the intense cold of the frigid zones and under the burning sun of the tropics; and if, from any cause, the body become incapable of keeping up its temperature when exposed to cold, or of moderating it when exposed to heat, death is the invariable result.

The production of animal heat is so closely connected with nutrition, that, in serious pathological modifications of this process, as in the essential fevers or extensive inflammations, the temperature of the body becomes an important guide, particularly in prognosis.

The study of the temperature in different classes of animals presents very great interest, but the limits of a work on pure human physiology restrict us to the phenomena as observed in man, and in animals in which the processes of nutrition are similar, if not identical. We shall therefore treat of the subject from one point of view and consider it as follows:

1. The normal temperature in the human subject, with its variations in different parts of the body and at different periods of life.

2. The diurnal variations in the animal temperature, and the relations of alimentation, digestion, respiration, nutrition, exercise, and the nervous system.

3. The means by which the temperature of the body is kept within the limits necessary to the preservation of life and health.

Limits of Variation in the Normal Temperature in Man.—A great number of observations have been made upon the normal temperature in the human subject under different conditions; but we shall cite those only in which all sources of error in thermometry seem to have been avoided, and in which the results present noticeable peculiarities. One of the most common methods of taking the general temperature has been to introduce a delicate thermometer, carefully protected from all disturbing conditions, into the axilla, reading off the degrees after the mercury has become absolutely stationary. Nearly all observations made in this way agree with the results obtained by Gavarret, who estimated that the temperature in the axilla, in a perfectly healthy adult man, in a temperate climate, ranges between 97·7° and 99·5° Fahr. Dr. Davy, from a large number of observations upon the temperature under the tongue, fixes the standard, in a temperate climate, at 98°. When we examine the temperature of the blood in the deeper vessels and the variations in different parts, we shall see that the axilla and the tongue, being more or less exposed to external influences, do not exactly represent the general heat of the organism; but these are the situations, particularly the axilla, in which the temperature is most frequently taken, both in physiological and pathological examinations. As a standard for comparison, we may assume that the most common temperature in these situations is 98°, subject to variations, within the limits of health, of about 0·5° below and 1·5° above.

Variations with External Temperature.—There can be no doubt that the general temperature of the body varies, though within very restricted limits, with extreme changes in climate. The results obtained by Davy, in a large number of observations in temperate and hot climates, show an elevation in the tropics of from 0·5° to 3°. It is well known, also, that the human body, the surface being properly protected, is capable of enduring for some minutes a heat much greater than that of boiling water. Under these conditions, the general temperature is raised but very slightly, as compared with the intense heat of the surrounding atmosphere. According to the observations of Dr. Dobson, the temperature was only raised to 99·5° in one instance, 101·5° in another, and 102° in a third, when the body was exposed to a heat of more than 212°. MM. Delaroche and Berger, however, found that the temperature in the mouth could be increased by from 3° to 9°, after sixteen minutes' exposure to intense heat. This was for the external parts only; but it is not at all probable that the temperature of the internal organs ever undergoes such extensive variations.

It is very difficult to estimate the temperature in persons exposed to intense cold, as in Arctic explorations, because the greatest care is always taken to protect the surface of the body as completely as possible; but experiments have shown that the animal heat may be considerably reduced, as a temporary condition, without producing death. In the latter part of the last century, Dr. Currie caused the temperature in a man to fall 15° by immersion in a cold bath; but he could not bring it below 83°. This extreme depression, however, lasted only two or three minutes, and the temperature afterward returned to within a few degrees of the normal standard. Nearly the same results were obtained by Hunter, in a series of experiments on a mouse. With an external temperature of 60°, he found the temperature in the upper part of the abdomen 99°, and in the pelvis, 96°. The animal was then exposed for an hour to a cold atmosphere of 13°, and there was a diminution of the temperature at the diaphragm of 16°, and at the pelvis, of 18°. These results show that, while the normal variations in the temperature in the human subject, even when exposed to great climatic changes, are very slight, generally not ranging beyond two degrees, the body may be exposed for a time to excessive heat or cold, and the extreme limits, consistent with the preservation of life, may be reached. As far as has been ascertained by direct experiment, these limits are 83° and 107°; giving a range of about 15° below and 9° above the average standard under normal conditions.

Variations in Different Parts of the Body.—It is to be expected that the temperature of the internal organs should be higher and more constant than that of parts, like the axilla or mouth, more or less exposed to loss of heat by evaporation and contact with the cool air; and the differences observed in the blood in certain parts, as in the two sides of the heart, have important bearings, as we shall hereafter show, upon the various theories of animal heat. We shall here simply note the variations observed in the blood in different situations and confine ourselves chiefly to late observations, which have generally been made with apparatus much more reliable and delicate than that which was formerly employed.

A great number of experiments have been made upon modifications in temperature accompanying the general change of the blood from arterial to venous; but perhaps the most exact and elaborate are those by M. Claude Bernard. For measuring the temperature in different parts of the vascular system, he used the exceedingly delicate "metastatic" thermometers of M. Walferdin; and in all comparative observations he employed the same instrument, introduced successively into different parts, frequently reversing the order and employing every precaution so as to insure perfectly physiological conditions. The preëminent skill of this distinguished observer in experimenting upon living animals is almost in itself a sufficient guarantee of the accuracy of his results.

It is universally admitted that the blood becomes slightly lowered in its temperature in passing through the general capillary circulation; but the amount of difference is ordinarily not more than a fraction of a degree, and it is dependent, in all probability, upon external conditions and the evaporation constantly going on from the surface of the body. This fact is not at all opposed to the proposition that the animal heat is generated in greatest part in the general capillary system, as one of the results of nutritive action; for the blood circulates with such rapidity that the heat acquired in the capillaries of the internal organs, where little or none is lost, is but slightly diminished before the fluid passes into the arteries, even in circulating through the lungs; and the evaporation from the surface simply moderates the heat acquired in the tissues and keeps it at the proper standard. We know that the heat of the body is equalized by means of the circulation and by cutaneous transpiration; and all comparative observations upon the temperature in different parts show that, where it is not subjected to refrigerating influences, the blood is warmer in the veins than in the arteries.

The elaborate investigations of Bernard have demonstrated that the blood is, as the rule, from 0·36° to 1·8° warmer in the hepatic veins than in the aorta. The temperature in the hepatic veins is from 0·18° to 1·44° higher than in the portal veins. These figures are the result of numerous experiments made upon dogs. The maximum of thirty-three observations upon the temperature in the aorta was 105·8°, and the minimum, 98·78°; the maximum of thirty-two observations upon the portal vein was 106·34°, and the minimum, 100·04°; the maximum of thirty-five observations upon the hepatic veins was 107°, and the minimum, 99·86°. Compared with the aorta, the temperature of the portal vein was generally found to be higher (maximum of difference, 0·9°); but, in a few instances (five out of fifteen), it was a very little lower, which is explained by Bernard upon the supposition that the intestinal canal is not entirely removed from external modifying influences. These results show that the blood coming from the liver is warmer than in any other part of the body.

The general fact that the superficial parts are cooler than those less exposed to loss of heat by evaporation does not demand extended discussion; but, in a series of experiments by Breschet and Becquerel, who were among the first to employ thermo-electric apparatus in the study of animal heat, it was found that the cellular tissue was from 2·5° to 3·3° cooler than the muscles. This difference will be readily understood when we consider the production of heat in the general system, and more especially in the highly-organized parts.

A most interesting question, in this connection, relates to the comparative temperature of the blood in the two sides of the heart. Upon this point there have been several conflicting observations, the results favoring two opposite theories of calorification. By some it has been thought that the blood gains heat in passing through the lungs, and this is explained by the theory of the direct union, in these organs, of oxygen with the hydro-carbons. Others suppose that the blood is slightly refrigerated in the air-cells. The questions here involved will be fully discussed in connection with the theories of animal heat; and we shall confine ourselves at present to a study of the experimental facts.

It is evident that, when the chest is opened, the external refrigerating influences might act differently upon the two sides of the heart, particularly as the right ventricle is much thinner than the left. It would not be improper, indeed, to exclude all observations made in this way, and to depend entirely upon experiments in which the physiological conditions are not so palpably violated. Magendie and Bernard introduced delicate thermometers into the two sides of the heart, through the vessels in the neck, without opening the chest. These experiments were made upon a horse, and the right heart was always found considerably warmer than the left. Hering introduced a thermometer into the cavities of the heart in a living calf affected with cardiac ectopia. The temperature of the right side was 102·74°, and the left side, 101·79°. Georg von Liebig illustrated one of the sources of error in all examinations made after opening the chest, by filling the cavities of the heart of a dog with warm water, placing the organ in a water-bath, and bringing the two sides to precisely the same temperature. After five minutes' exposure to the air, the temperature in the right ventricle was sensibly lower than in the left, which was undoubtedly due to the difference in the thickness of the ventricular walls. The observations by Bernard himself upon dogs and sheep are very conclusive, as far as these animals are concerned. In dogs he found a difference of from 0·1° to 0·2°, always in favor of the right side; and the results in sheep were nearly the same. These experiments are only indirectly applicable to the human subject; and if it be proven that, in animals, the conditions vary with "the state of the skin, the digestive apparatus, and the muscular system" (Colin), it is impossible, in the absence of positive demonstration, to say what change in temperature, if any, takes place in the blood in its passage through the lungs. The only reliable observations upon this point in man are those made by Prof. Lombard, of Boston. Prof. Lombard used in his experiments a very ingenious and delicate thermo-electric apparatus, capable of indicating a difference of $\frac{1}{5000}$ of a degree cent. With this instrument, he was able to determine very slight variations in the temperature of the blood in the arterial system, by simply placing the conductors over any of the superficial vessels, like the radial. Of course it is impossible to note the actual temperature in the two sides of the heart in the human subject during life; but Prof. Lombard endeavored to arrive at the same end, by calculating that, if all the sources of refrigeration in the lungs were artificially removed, the blood in the arteries should gain about the same amount of heat that would be lost under ordinary conditions. To effect this object, he breathed air saturated with moisture and of the same temperature as the circulating blood. "If, then, when respiration takes place under ordinary circumstances, the blood is cooled one-third of a degree (cent.) in passing through the lungs, the temperature should be raised so much; that is to say, one-third of a degree, when we respire air at the temperature of the blood and saturated with the vapor of water, all loss of heat then being impossible." In numerous experiments performed upon this principle, Prof. Lombard failed to observe a sufficiently marked elevation of temperature to justify the conclusion that the blood is ordinarily cooled in passing through the lungs. These experiments cannot be so positive as those made by introducing thermometers into the heart in living animals without opening the chest or disturbing the circulation; but they are important, in connection with such observations, as failing to prove that the blood is either cooled or heated in the lungs. From these facts it appears that there is no positive evidence of any change in the temperature in the blood in passing through the lungs in the human subject. In animals there probably exist no constant differences in temperature in the two sides of the heart. When the loss of heat by the general surface is active, as in animals with a slight covering of hair, the blood is generally cooler in the right cavities; but, in animals with a thick covering, that probably lose a great deal of heat by the pulmonary surface, the blood is cooler upon the left side. There can be no doubt that there are refrigerating influences in the lungs, both from the low temperature of the inspired air and from evaporation; but these are equalized and sometimes overcome by processes in the blood itself, although, as we shall see hereafter, the lungs are by no means the most important organs of calorification.

Variations at Different Periods of Life.—The most important variations in the temperature of the body at different periods of life are observed in infants just after birth. Aside from one or two observations, which are admitted to be exceptional, the body of the infant and of young mammalia and birds, removed from the mother, presents a diminution in temperature of from one to nearly four degrees. In infancy the ability to resist cold is less than in later years; but after a few days the temperature of the child nearly reaches the standard in the adult, and the variations produced by external conditions are not so great.

The experiments of W. F. Edwards have an important bearing upon our ideas of nutrition during the first periods of extra-uterine life. He found that, in certain animals, particularly dogs and cats, that are born with the eyes closed and in which the foramen ovale remains open for a few days, the temperature rapidly diminished when they were removed from the body of the mother, and that they then become reduced to a condition approximating that of cold-blooded animals; but, after about fifteen days, this change in temperature could not be effected. In dogs just born, the temperature fell after three or four hours' separation from the mother to a point but a few degrees above that of the surrounding atmosphere. The views advanced by Edwards are fully illustrated in instances of premature birth, when the animal heat is much more variable than in infants at term, and in cases of persistence of the foramen ovale. In certain instances in which life has been prolonged under this abnormal condition, the individual is nearly in the condition of a cold-blooded animal. We can also understand the remarkable power of resistance to asphyxia in newly-born animals, for it is well known that cold-blooded animals will bear deprivation of oxygen much better than the higher classes.

In adult life there does not appear to be any marked and constant variation in the normal temperature; but, in old age, according to the observations of Davy, while the actual temperature of the body is not notably reduced, the power of resisting refrigerating influences is diminished very considerably.

There are no positive observations showing any constant differences in the temperature of the body in the sexes; and it may be assumed that, in the female, the animal heat is modified by the same influences and in the same way as in the male.

Diurnal Variations in the Temperature of the Body.—Although the limits of variation in the animal temperature are not very extended, certain fluctuations are observed, depending upon repose or activity, digestion, sleep, etc., which it is necessary to take into account. These conditions, which are of a perfectly normal character, may induce changes in the temperature amounting to from one to three degrees. It has been ascertained that there are two well-marked periods in the day when the heat is at its maximum. These, according to the most recent observations in Germany, are at eleven A. M. and four P. M.; and it is a curious fact, that, while all observations agree upon this point, the very elaborate experiments of Lichtenfels and Fröhlich show that these periods are well marked, even when no food is taken. Bärensprung and Ladame farther show that the fall in temperature during the night takes place sleeping or waking; and that when sleep is taken during the day it does not disturb the period of the maximum, which occurs at about four P. M. According to these experiments, at eleven in the morning, the animal heat is at one of its periods of maximum; it gradually diminishes for two or three hours and is raised again to the maximum at about four in the afternoon, when it again undergoes diminution until the next morning. The variations amount to from about 1° to 2·16.° The minimum is always during the night.

The relations of the animal temperature to digestion are still somewhat indefinite. It is well known that activity of the digestive organs increases the consumption of oxygen, and, to a corresponding degree, the exhalation of carbonic acid; but we have to assume that the production of heat is in direct ratio to the respiratory action in order to establish any relation between calorification and the digestion of ordinary food. It is easy to calculate that a given amount of oxygen will produce a definite quantity of carbonic acid, and will, by its union with carbon and hydrogen, generate a certain number of "units of caloric;" but the mechanism of the production of animal heat is too complex and not well enough understood to admit of such positive reasoning. There is, indeed, no experimental evidence of any marked and constant change in the general temperature of the body during the ordinary process of digestion; but it is none the less true that the quantity and quality of food bear a certain relation to calorification. This is inevitable from the connection of animal heat with the general process of nutrition; but this relation is expressed in the connection of calorification with nutrition of the tissues, and not in the process of the digestion or absorption of food. We shall see that, when nutrition is modified by alimentation, the general temperature is always more or less affected; and when the requirements of the system, as far as the generation of heat is concerned, are changed, by climate or otherwise, alimentation is modified. One of the objects of alimentation and nutrition is to maintain the body at a nearly constant temperature.

The influence of defective nutrition or inanition upon the heat of the body is very marked. John Hunter, in his experiments upon animal heat, made a few observations upon this point and noted a decided fall in temperature in a mouse kept fasting. The same phenomena were also observed by Collard de Martigny; and Chossat noted the effects of deprivation of food upon the power of maintaining the animal temperature, in the most exact and satisfactory manner. In pigeons, the extreme diurnal variation in temperature, under normal conditions, was found by Chossat to be 1·3.° During the progress of inanition, the daily variation was increased to 5·9,° with a slight but well-marked diminution in the absolute temperature; and the periods of minimum temperature were unusually prolonged. Immediately preceding death from starvation, the diminution in temperature became very rapid, the rate, in the observations on turtle-doves, being from 7° to 11° per hour. Death usually occurred when the diminution had amounted to about 30°.

When the surrounding conditions call for the development of an unusual amount of heat, the diet is always modified, both as regards the quantity and kind of food; but when food is taken in sufficient quantity and is of a kind capable of maintaining proper nutrition, its composition does not affect the general temperature. If we were to adopt without reserve the view that the non-nitrogenized alimentary principles are the sole agents in the production of heat, we should certainly be able to determine either an increase in the animal heat or a greater loss of heat from the surface, in persons partaking largely of this kind of food. This, however, has not been shown to be true; and the temperature of the body seems to be uniform in the same climate, even in persons living upon entirely different kinds of food. The elaborate observations of Dr. Davy are very conclusive upon this point: "The similarity of temperature in different races of men is the more remarkable, since between several of them whose temperatures agreed, there was nothing in common but the air they breathed—some feeding on animal food almost entirely, as the Vaida—others chiefly on vegetable diet, as the priests of Boodho—and others, as Europeans and Africans, on neither exclusively, but on a mixture of both." Nevertheless, the conditions of external temperature have a remarkable influence upon the diet. It is well known, for example, that, in the heat of summer, the amount of meats and fat taken is relatively small, and the succulent, fresh vegetables and fruits, large, as compared with the diet in the winter. But although the proportion of starchy matters in many of the fresh vegetables used during a short season of the year is not large, these articles are equally deficient in nitrogenized matter. During the winter, the ordinary diet, composed of meat, fat, bread, potatoes, etc., contains a large amount of nitrogenized substance, as well as a considerable proportion of the hydro-carbons; and, in the summer, we instinctively reduce the proportion of both of these varieties of principles, the more succulent articles taking their place. This is even more strikingly illustrated by a comparison of the diet in the torrid or temperate and in the frigid zone. Under the head of alimentation, we have already noted the prodigious quantities of food consumed in the Arctic regions and the effect of the continued cold upon the habits of diet of persons accustomed to a temperate climate. It is stated, upon undoubted authority, that the daily ration of the Esquimaux is from twelve to fifteen pounds of meat, about one-third of which is fat. Dr. Hayes, the Arctic explorer, noted that, with a temperature ranging from −60° to −70,° there was a continual craving for a strong, animal diet, particularly fatty substances. Some of the members of the party were in the habit of drinking the contents of the oil-kettle with evident relish.

Under such conditions as those which surround inhabitants of temperate regions, in passing into the frigid zones a change in diet is imperatively demanded, in order to keep the animal temperature at the proper standard; but, when the climate is changed from the temperate to the torrid, the habits of life frequently remain the same. It is a pretty general opinion among physicians who have studied the subject specially, that many of the peculiar disorders that affect those who have changed their residence from a temperate to a very warm climate are due, in a great measure, to the fact that the diet and habits of life are unchanged.

The influence of alcoholic beverages upon the animal temperature has been studied chiefly with reference to the question of their use in enabling the system to resist excessive cold. We have already discussed somewhat fully the physiological effects of alcohol, and we have seen that its use does not enable men to endure a very low temperature for a great length of time. This is the universal testimony of scientific Arctic explorers; and Dr. Hayes particularly states, that, "in almost any shape, it is not only completely useless, but positively injurious."

The relations of animal heat to respiration and nutrition constitute a most interesting and important division of the subject, which will be more fully considered in discussing the various theories of calorification. As a rule, when the respiratory activity is physiologically increased, as it is by exercise, bodily or mental, ingestion of food, or by diminished external temperature, the generation of heat in the body is correspondingly augmented; and, on the other hand, it is diminished by conditions which physiologically decrease the absorption of oxygen and the exhalation of carbonic acid.

The relations of animal heat to the general process of nutrition are most intimate. Any condition that increases the activity of nutrition and of disassimilation, or even any thing that increases disassimilation alone, will increase the production of heat. The reverse of this proposition is equally true. In pathology, the heat of the body may be increased by a deficient action of the skin in keeping down the temperature, without any increase in the activity of calorification.

Influence of Exercise, etc., upon the Heat of the Body.—The influence of muscular activity upon animal heat is peculiarly interesting in connection with the theories of calorification, from the fact that the muscular system constitutes the greatest part of the organism; and, as has repeatedly been shown by experiment, a muscle taken from a living animal is not only capable of contraction upon the application of a stimulus, but it will perform for a time certain of the acts of nutrition and disassimilation, such as the appropriation of oxygen and the generation and exhalation of carbonic acid.

The most complete repose of the muscular system is observed during sleep, when hardly any of the muscles are brought into action, except those concerned in tranquil respiration. There is always a notable diminution in the general temperature at this time. This fact has been observed by all who have studied the question experimentally. In the diurnal variations in the temperature of the body, the minimum is always during the night; and, as we have already seen, this is not entirely dependent upon sleep, for a depression in temperature is constantly observed at that time, even when sleep is avoided.

It is a matter of common observation, that one of the most efficient methods of resisting the depressing influence of cold is to constantly exercise the muscles; and it is well known that, after long exposure to intense cold, the tendency to sleep, which becomes almost irresistible, if indulged in, is followed by a very rapid loss of heat and almost certain death. It is not necessary to cite the accounts of travellers and others in support of these facts. In some animals, the amount of increase in the temperature during muscular activity is very great, and this is notably marked in the class of insects. In the experiments of Newport, upon bees and other insects, a difference of about 27° was noted between the conditions of complete repose and great muscular activity. These facts are interesting, as showing the very great elevation of temperature that can be produced in the lower order of beings during violent excitement; but, in man, the differences, although distinct, are never very considerable, for the reason that violent muscular exertion is generally attended with greatly-increased action of the skin, which keeps the heat of the body within very restricted limits. In the experiments of Newport, the loss of heat from the surface was arrested by confining the insects in small glass bottles.

The effects of active exercise, as in fast walking or riding, were very well observed by Dr. Davy. He found a constant elevation in the general temperature (taken under the tongue), amounting to between one and two degrees; but the most marked effects were observed in the extremities, especially when they were cold before taking the exercise.

The elevation in temperature that attends muscular action is produced directly in the substance of the muscle. This important fact was settled by the very interesting and ingenious experiments of Becquerel and Breschet. Introducing a thermo-electric needle into the biceps of a man who used the arm in sawing wood for five minutes, these physiologists noted an elevation of temperature of one degree centigrade (nearly two degrees Fahr.). The production of heat in the muscular tissue was even more strikingly illustrated by Matteucci, in experiments with portions of muscle from the frog. Not only did he observe absorption of oxygen and exhalation of carbonic acid after the muscle had been removed from the body of the animal, but he noted an elevation in temperature of about one degree Fahr., following contractions artificially excited.

It is useless to multiply citations of experiments illustrating the facts above noted or to discuss elaborately the theoretical transformation of a given quantity of caloric into a definite and an invariable amount of work. The conditions in the animal economy are such that we cannot exactly appreciate the loss of heat by the cutaneous and respiratory surfaces; nor can we follow the processes in the body which involve the disappearance of oxygen and the evolution of carbonic acid; the exact changes undergone by the hydro-carbonaceous elements of food and constituents of the body; the amount of heat involved in the changes of the nitrogenized elements; and, in short, we cannot make the corrections that are absolutely necessary before we can hope to reduce the question of the oxidation of certain principles in the body, the development of heat, and the generation of mechanical force, to exact mathematical calculation.

Observations upon the influence of mental exertion on the temperature of the body have not been so numerous, but they are, apparently, no less exact in their results. Dr. Davy was the first to make any extended experiments upon this point and has noted a slight but constant elevation during "excited and sustained attention." The same line of observation has been followed by Prof. Lombard, who employed much more exact methods of investigation. Prof. Lombard noted an elevation of temperature in the head during mental exertion of various kinds, but it was slight, the highest rise not exceeding the twentieth of a degree. It is stated, also, that the temperature of the body is increased by the emotions of hope, joy, anger, and all exciting passions, while it is diminished by fear, fright, and mental distress. Burdach, from whom the foregoing statement is taken, cites an example of an elevation of temperature from 96° to 99·5° in a violent access of anger, and a descent to 92·75° under the influence of fear, but the temperature soon returned to 97·25°.

The nervous system exerts a most important influence over the animal temperature, as it modifies the circulation and the nutritive processes in particular parts. The most interesting of these influences are transmitted through the sympathetic system. These will be discussed, to a certain extent, in connection with the theories of calorification; but they cannot be taken up fully until we come to consider the functions of the sympathetic system and its relations to nutrition. In this connection, we shall simply allude to certain phenomena manifested through the nervous system, without attempting to fully explain their mechanism.

It is well known that, when the sympathetic nerves going to a particular part are divided, the arterial coats are paralyzed and dilated, the supply of blood is increased, nutrition is locally exaggerated and more or less modified, and the temperature of the part is increased by from five to ten degrees. An illustration of these facts in the ear of the rabbit, after division of the sympathetic in the neck, is a very common observation, which we have often verified in public demonstrations. All of these unnatural phenomena disappear upon galvanization of the divided extremity of the nerve. These local modifications in the temperature have been frequently observed pathologically in the human subject. A number of curious local variations of temperature can be explained by direct or reflex action through the sympathetic nerves.

It is evident that, if animal heat be one of the necessary attendant phenomena of nutrition, it must be greatly influenced by conditions of the circulation. It has been a question, indeed, whether the modifications in temperature produced by operating upon the sympathetic system of nerves be not due entirely to changes in the supply of blood. It is certain that whatever determines an increased supply of blood to any part raises the temperature; and, whenever the quantity of blood in any organ or part is considerably diminished, the temperature is reduced. This fact is constantly illustrated in operations for the deligation of large arteries. It is well known that, after tying a large vessel, the utmost care is necessary to keep up the temperature of the part to which its branches are distributed, until the anastomosing vessels become enlarged sufficiently to supply the amount of blood necessary for healthy nutrition.

Sources of Animal Heat.

The most interesting question connected with calorification relates to the sources of heat in the living organism; and a careful estimate of the physiological value of all the facts that have been positively established with reference to this point places the following proposition beyond any reasonable doubt:

The generation of heat in the living animal organism is connected, more or less intimately, with all of the processes of nutrition and disassimilation, including, of course, the consumption of oxygen and the production of carbonic acid; and this function is modified, to a greater or less degree, by all conditions that influence the general process of nutrition or the operation of the nutritive forces in particular parts.

This proposition is not contradicted by any well-settled physiological facts or principles. Every one of the functions of the body bears more or less closely upon nutrition; and all the physiological modifications of the various functions, without exception, affect the process of calorification. We must bear in mind the fact that, in man and in the warm-blooded animals generally, the maintenance of the temperature of the organism at a nearly fixed standard is a necessity of life and of the physiological action of the different parts; and that, while heat is generated in the organism with an activity that is constantly varying, it is as constantly counterbalanced by physiological loss of heat from the cutaneous and the respiratory surfaces. Variations in the activity of calorification are not to be measured by corresponding changes in the temperature of the body, but are to be estimated by calculating the amount of heat lost. The ability of the human race to live in all climates is explained by the adaptability of man to different conditions of diet and exercise, and to the power of regulating loss of heat from the surface by appropriate clothing.

Our proposition regarding the production of animal heat is in no wise opposed to the so-called combustion-theory, as it is received by most physiologists of the present day; but it must be admitted that it is an unfortunate use of terms to apply the name combustion to the general process of nutrition, as is done by those who attempt to preserve, not only the ideas of the great author of this theory, but certain modes of expression, which were in accordance only with his limited knowledge of the phenomena of nutrition. If we speak of animal heat as the result of combustion of certain elements, it will be necessary either to refer constantly to the difference between combustion as it occurs in the organism and mere oxidation out of the body, or to start with a full lefinition of what is to be understood by the term physiological combustion, which educes itself simply to a definition of nutrition. Regarding calorification, then, as connected with all of the varied processes of nutrition, it remains for us to determine the ollowing questions:

1. In what part or parts of the organism is heat generated?
2. What is the relative importance in calorification, as regards the amount of heat enerated, of the processes of nutrition, as we can study them separately?
3. What are the principles invariably and of necessity consumed and produced in the rganism in calorification; and what is the relative importance of the principles thus onsumed and the products thus generated and thrown off?
4. How far have we been able to follow those material transformations in the organ-m which involve the consumption of certain principles, the production of new comounds, and the generation of heat?

Seat of the Production of Animal Heat.—Few if any physiologists at the present ay hold to the opinion that there is any part or organ in the body specially and exclusively concerned in the production of heat. In the early history of the oxidation-theory of Lavoisier, it was thought by some that the inspired oxygen combined with the hydro-carbons of the blood in the lungs, and that the heat of the body was generated almost exclusively in these organs; but this idea has long since been abandoned. We have already fully considered the question of the loss or gain in the temperature of the blood in its passage through the lungs, and we have seen that there is, to say the least, no constant elevation showing a generation of heat in these organs, sufficient to warm the blood, and through it the different parts of the body. If we find that the blood in coming from the lungs has about the same temperature as when it entered these organs, it must be admitted that there is a certain generation of heat to compensate the loss by evaporation from the pulmonary surface. As far as we know, the heat that results from the mere physical solution of oxygen in the blood is all that is produced in the lungs. There is no sufficient evidence to show that the lungs are special organs of calorification; and any generation of heat that takes place here is due, probably, to purely physical phenomena in the blood.

It is only necessary to refer back to the pages treating of the variations in the temperature of the blood in different parts, to show that heat is produced in the general system and not in any particular organ or in the blood as it circulates. The experiments of Matteucci, showing an elevation of temperature in a muscle excited to contraction after it had been removed from the body, and the observations of Becquerel and Breschet, showing increased development of heat by muscular contraction, are sufficient evidence of the production of heat in the muscular system; and, inasmuch as the muscles constitute by far the greatest part of the weight of the body, they are a most important source of animal heat.

It has been demonstrated, by the experiments of Bernard, that the blood becomes notably warmer in passing through the abdominal viscera. This is particularly marked in the liver, and it shows that the large and highly-organized viscera are also important sources of caloric.

As far as it is possible to determine by experimental demonstration, not only is there no particular part or organ in the body endowed with the special function of calorification, but every part in which the nutritive forces are in operation produces a certain amount of heat; and this is probably true of the blood-corpuscles and other anatomical elements of this class. The production of heat in the body is general and is one of the necessary consequences of the process of nutrition; but, with nutrition, it is subject to local variations, as is strikingly illustrated in the effects of operations upon the sympathetic system of nerves and in the phenomena of inflammation.

Relations of Animal Heat to Nutrition.—Nutrition involves the appropriation of matters taken into the body and the production and elimination of effete substances. In its widest signification, this includes the consumption of oxygen and the elimination of carbonic acid; and, consequently, we may strictly regard respiration as a nutritive act. All of the nutritive processes go on together, and they all involve, in most warm-blooded animals at least, a nearly uniform temperature. During the first periods of embryonic life, the heat derived from the mother is undoubtedly necessary to the development of tissue by a change of substance, analogous to nutrition and even superior to it in activity. During adult life, animal heat and the nutritive force are coexistent. It now becomes a question to determine whether there be any class of nutritive principles specially concerned in calorification, or any of the nutritive acts, that we have been able to study by themselves, which are exclusively or specially directed to the maintenance of the temperature of the body. These questions simply involve a review of considerations with regard to the relations of various of the functions to the production of heat.

The supply of the waste of tissue being effected by metamorphosis of alimentary matter —a process, the exact nature of which we have not been able to determine—it has thus far been possible, only, to divide the food into different classes. Of these, leaving out oxygen, we shall consider, in this connection, the organic matters, divided into nitrogenized and non-nitrogenized. The inorganic salts are always combined with nitrogenized matter, and they seem to pass through the organism without undergoing any considerable change; and there is no evidence that they have any connection, of themselves, with the production of heat.

What is the relation to calorification of those processes of nutrition which involve the consumption of nitrogenized matter and the production of the nitrogenized excrementitious principles?

We cannot study the phenomena of calorification alone, isolated from the other acts of nutrition. We may confine an animal to a purely nitrogenized diet, and the heat of the body will be maintained at the proper standard; but at all times there is a certain quantity of non-nitrogenized matter (sugar and perhaps fat) produced in the system, which is formed only to be consumed. We may starve an animal, and the temperature will not fall to any very great extent until a short time before death. Here we may suppose that the process of deposition of nutritive matter in the tissues from the blood is inconsiderable, as compared with the transformation of the substance of these tissues into effete matter; and it is almost certain that non-nitrogenized matter is not produced in the organism in quantity sufficient to account, by its destruction in the lungs, for the carbonic acid exhaled. It seems beyond question that there must be heat evolved in the body by oxidation of nitrogenized matter. When the daily amount of food is largely increased for the purpose of generating the immense amount of heat required in excessively cold climates, the nitrogenized matters are taken in greater quantity, as well as the fats, although their increase is not in the same proportion. When, however, we endeavor to assign to the nitrogenized matters a definite proportion of heat-producing power, we are arrested by a want of positive knowledge with regard to the metamorphoses which these principles undergo; and it is equally impossible to fix the relative calorific value of the deposition of new material in repair of the tissues and the change of their substance into effete matter in disassimilation. From these facts, and from other considerations that have already been fully discussed under different heads, it is evident that the physiological metamorphoses of nitrogenized matter bear a certain share in the production of animal heat; although, in connection with inorganic matter, their chief function seems to be the repair of the tissues endowed with so-called vital properties.

What is the relation of the consumption of non-nitrogenized matter to the production of animal heat?

It has been impossible to treat of the relations of the non-nitrogenized elements to nutrition without considering more or less fully the part which these principles bear in the production of heat; and we must refer the reader to the previous pages for a discussion of certain of these points. In this connection, we shall simply state the relations that this class of principles is known to bear to calorification, and the facts upon which our statements are based.

It has been pretty clearly shown that both sugar and fat are actually produced in the organism, even when the diet is strictly nitrogenized in its character; but we shall consider only the relations of the non-nitrogenized elements introduced into the body, assuming that the principles of this class appearing *de novo* in the organism are the result of a transformation of nitrogenized substances.

As far as the destination of the amylaceous, saccharine, and fatty elements of food is concerned, we only know that they are incapable, of themselves, of repairing muscular tissue, and that they cannot sustain life. They are never discharged from the body in health in the form under which they enter; but they are in part or completely destroyed in nutrition. They are completely destroyed in persons who, from habitual muscular exercise, have very little adipose tissue. When their quantity in the food is large, they are not of necessity entirely consumed, but they may be deposited in the form of adipose tissue.

This, however, may be made to disappear by violent exercise or under an insufficient diet.

There can be no doubt that the non-nitrogenized class of alimentary principles is craved by the system in long-continued exposure to extreme cold. This is particularly marked with regard to the fats. In all cold climates, fat is a most important element of food; and, in excessively cold regions, while the nitrogenized elements are largely increased, there is a very much larger proportional increase in the quantity of fat. These facts are very significant. If the non-nitrogenized elements of food—which are not always indispensable, though often very necessary articles—do not form tissue, are not discharged from the body, and are consumed in some of the processes of nutrition, it would seem that their change must involve the production of carbonic acid, perhaps also of water, and the evolution of heat. It is so difficult to ascertain the exact quantities of carbonic acid, watery vapor, etc., thrown off by the lungs, skin, and other emunctories, and to estimate the exact amount of heat produced and lost, that it is not surprising that calculations of the calorific power of different articles of food should be frequently erroneous; particularly as we have no means of knowing the exact calorific value of the nitrogenized principles.

Although we may assume that the non-nitrogenized elements of food are particularly important in the production of animal heat, and that they are not concerned in the repair of tissue, it must be remembered that the animal temperature may be kept at the proper standard upon an exclusively nitrogenized diet; and we cannot, indeed, connect calorification exclusively with the consumption of any single class of principles or with any single one of the acts of nutrition.

Relations of Calorification to Respiration.—Respiration is one of the nutritive processes that can be closely studied by itself, as it involves the appropriation by the system of a single principle (oxygen), and that simply in solution in the blood. There can be no doubt that, of all the nutritive acts, respiration is, far more than any other, intimately connected with calorification. As far as the general process is concerned, the production of heat is usually in direct ratio to the consumption of oxygen and the exhalation of carbonic acid. In the animal scale, wherever we have the largest amount of heat produced, we observe the greatest respiratory activity. In man, whatever increases the generation of heat increases as well the consumption of oxygen and the elimination of carbonic acid. The production of heat in warm-blooded animals is constant, and it cannot be interrupted, even for a few minutes. The same is true of respiration. The tissues may waste for want of nourishment, but the heat of the body must be kept near a certain standard, which is almost always much higher than the surrounding temperature; and there is no other nutritive act so constant and so immediately necessary to existence as the appropriation of oxygen. It is not surprising, then, that, early in the history of the physiology of nutrition, before we knew even the exact condition and proportion of the gases in the blood, it should have been thought that animal heat was the result of slow combustion of the hydro-carbons.

The physiological history of respiration and of animal heat dates from the same series of discoveries. In the latter part of the last century, the great chemist, Lavoisier, discovered the intimate nature of the respiratory process and applied the theory of the consumption of oxygen and the evolution of carbonic acid to calorification. Like nearly all of the great advances in physiological science, the distinctly-enunciated idea was foreshadowed by earlier writers. It will not be necessary to treat, from a purely historical point of view, of the discoveries made by Lavoisier. He undoubtedly went as far in his explanations of the phenomena of animal heat as was possible in the condition of the science at the time his investigations were made; and, although he inevitably fell into some errors in his calculations and deductions, he must forever be regarded as the author of the first reasonable theory of the generation of heat by animals.

The Consumption of Oxygen and Production of Carbonic Acid in Connection with the Evolution of Heat.—As far as it has been possible to determine by actual experiment, all animals, even those lowest in the scale, appropriate oxygen and eliminate carbonic acid. This is equally true of all living tissues; and, since it has been ascertained that oxygen is dissolved, as oxygen, in the arterial blood, that it disappears in part or entirely in the capillary circulation, that carbonic acid is taken up by the venous blood, both in solution and in feeble combination in the bicarbonates, to be discharged in the lungs by displacement and the action of the pneumic acid, and that the tissues themselves have the property of appropriating oxygen and exhaling carbonic acid, those who adopt the theory of Lavoisier have simply changed the seat of oxidation from the lungs to the general system.

It has been proven beyond question that oxygen, of all the principles introduced from without, is the one most immediately necessary to nutrition; and it differs from the class of substances ordinarily known as alimentary, only in the fact that it is consumed more promptly and constantly. In the same way, carbonic acid is to be regarded as an element of excretion, like urea, creatine, etc., differing from them only in the immediate necessity for its elimination. As the comparatively slow excretion of urea and other nitrogenized matters is connected with the ingestion of ordinary alimentary substances that are slowly appropriated by the tissues, so the rapid elimination of carbonic acid is connected with the equally rapid appropriation of oxygen. There is no reason why we should not regard carbonic acid, like other effete substances, as an excretion, the result of disassimilation of the tissues generally; but, more closely than any, it is connected with the rapid and constant evolution of heat.

Experiments on the influence of the sympathetic nerves upon the temperature of particular parts have completed the chain of evidence in favor of the localization of the heat-producing function in the tissues. It is not our purpose to discuss the relations of the sympathetic system to nutrition, deferring this subject until we come to treat specially of the nervous system; but the facts bearing on calorification are briefly as follows:

If the sympathetic nerve be divided in the neck of a rabbit or any other warm-blooded animal, the side of the head supplied by this nerve will become from five to eight or ten degrees warmer than the opposite side, or than the rest of the body. This observation we have repeatedly verified. The conditions under which this local exaggeration of the animal heat is manifested are, dilatation of the arteries of supply of the part, so that it receives very much more blood than before, and increased activity in the general process of nutrition. It also has been observed, in experiments upon the horse, that the blood coming from the part is red and contains very much more oxygen than ordinary venous blood.

The observations of MM. Estor and Saint-Pierre show that the blood coming from inflamed parts, in which there is a considerable elevation above the normal temperature, is red, and that it contains from fifty to two hundred and fifty per cent. more oxygen than ordinary venous blood. These facts are regarded as inconsistent with the view that the temperature of parts is due chiefly to oxidation; but, when we consider the fact that, in the conditions above mentioned, the actual quantity of blood circulating in these parts is increased many times, the error in the deduction is palpable enough. It is not sufficient to show that the blood coming from an inflamed tissue, with an abnormally high temperature, contains more oxygen than under ordinary conditions, but it is indispensable to demonstrate that the absolute quantity of oxygen consumed is diminished. For example, if the venous blood should contain double the normal proportion of oxygen, but the quantity coming from the part should be increased threefold, it is evident that the actual consumption of oxygen would be doubled. As an illustration, let us assume that, in one minute, 100 parts of blood, containing 10 parts of oxygen, circulate through a member, losing in its passage 7·5 parts of oxygen, thus leaving a proportion of 2·5 of oxygen for the venous blood; if the part become inflamed, let us suppose that, during the same period, 300 parts of blood, with 30 parts of oxygen, pass through, but that the venous blood contains five per cent. of oxygen, or 15 parts. That would show an actual consumption of 15 parts of oxygen in inflammation, against 7·5 under normal nutritive conditions. Estor and Saint-Pierre do not state the amount of increase in the quantity of blood circulating through inflamed tissues, but they admit that, "in inflammation, the vessels are dilated, and the current of blood is more rapid." An increase in the absolute quantity of blood passing through parts after division of the sympathetic nerves distributed to the coats of the blood-vessels has been observed by all who have experimented upon the subject; and the increase is probably greater than that which we have assumed in our argument. An additional argument in favor of our interpretation of the experiments of Estor and Saint-Pierre is the fact, noted by them, that the blood from inflamed parts contains more carbonic acid than ordinary venous blood.

Taking into account all the facts bearing upon the question, there can be little doubt, that, while the processes of nutrition and disassimilation, involving changes in the nitrogenized constituents of the blood and the tissues, are not disconnected with calorification, the production of heat by animals is most closely related to the appropriation of oxygen and the formation of carbonic acid.

Intimate Nature of the Calorific Processes.—A comprehension of the intimate nature of the calorific processes involves simply an answer to the question, how far we can follow the material transformations in the organism, which involve the consumption of certain principles, the production of new compounds, and the evolution of heat. As regards the nature of the intermediate processes connecting the disappearance of oxygen with the production of carbonic acid, we can only explain it by reciting the simple facts. Oxygen disappears, carbonic acid is formed, and the carbon is furnished, perhaps by the tissues, perhaps by the blood, probably by both. It is probable that the intermediate changes are more simple and rapid than those which intervene between the appropriation of nitrogenized nutritive matter and the formation of the nitrogenized excretions; but we have never been able to follow either of these processes through all of its different phases. We must be content, in the present condition of our positive knowledge, to regard calorification as one of the attendant phenomena of nutrition; and we have only to study as closely as possible the facts with regard to the disappearance of certain principles and the formation of effete matters, that are always and of necessity associated with the development of heat.

Equalization of the Animal Temperature.—A study of the phenomena of calorification in the human subject has shown that under all conditions of climate the general heat of the body is equalized. Nearly always, the surrounding temperature is below the standard of heat of the body, and there is, of necessity, an active production of caloric. Under all conditions, there is more or less loss of heat by evaporation from the general surface; and, when the surrounding atmosphere is very cold, it becomes desirable to reduce this loss to the minimum. This is done by appropriate clothing, which must certainly be regarded as a physiological necessity. The proper kind of clothing, the conducting power of different materials, their porosity, etc., form important questions in practical hygiene, and their full discussion belongs to special treatises. Clothing protects from excessive heat as well as from cold. Thin, porous articles moderate the heat of the sun, equalize evaporation, and afford great protection in hot climates. In excessive cold, clothing is of the greatest importance in preventing the escape of heat from the body. When the body is not exposed to currents of air, the garments are useful chiefly as non-conductors, imprisoning many layers of air, which are warmed by contact with the person. It is farther very important to protect the body from the wind, which increases so greatly the loss of heat by evaporation. It is wonderful, however, how intense a cold may be resisted by healthy men under proper conditions of alimentation and exercise and with the protection of appropriate clothing, as in Arctic explorations, when the thermometer has for days ranged from −60° to −70° Fahr.

When from any cause there is a tendency to undue elevation of the heat of the body, cutaneous transpiration is increased, and the temperature is kept at the proper standard. We have already considered this question in treating of the action of the skin, and we have noted facts showing that men can work when exposed to a heat much higher than that of the body itself. The amount of vapor that is lost under these conditions is sometimes enormous, amounting to from two to four pounds in an hour. We have ourselves often noted a loss of between two and three pounds after exposure for less than an hour to a steam-bath of from 110° to 116° ; and a much greater elevation of temperature, in dry air, can be tolerated with impunity. We have alluded to some of the observations upon the temperatures that could be borne without bad results, in connection with the question of variations in the heat of the body. In the experiments of Delaroche and Berger, the temperature was considerably under 200°. Tillet recorded an instance of a young girl who remained in an oven for ten minutes without inconvenience, at a temperature of 130° Réaumur, or 324·5° Fahr. Dr. Blagden, in his noted experiments in a heated room, made in connection with Drs. Banks, Solander, Fordyce, and others, found, in one series of observations, that a temperature of 211° could be easily borne ; and, at another time, the heat was raised to 260°. Chabert, who exhibited in this country and in Europe under the name of the "fire-king," is said to have entered ovens at from 400° to 600°. Under these extraordinary temperatures, the body is protected from the radiated heat by clothing, the air is perfectly dry, and the animal temperature is kept down by excessive exhalation from the surface.

It is a curious fact, that, after exposure of the body to an intense dry heat or to a heated vapor, as in the Turkish or Russian baths, when the general temperature is somewhat raised and the surface is bathed in perspiration, a cold plunge, which checks the action of the skin almost immediately, is not injurious and is decidedly agreeable. This presents a striking contrast to the effects of sudden cold upon a system heated and exhausted by long-continued exertion. In the latter instance, when the perspiration is suddenly checked, serious disorders of nutrition, inflammations, etc., are very liable to occur. The explanation of this, as far as we can present any, seems to be the following: When the skin acts to keep down the temperature of the body in simple exposure to external heat, there is no modification in nutrition, and the tendency to an elevation of the animal temperature comes from causes entirely external. It is a practical observation that no bad effects are produced, under these circumstances, by suddenly changing the external conditions; but, when the animal temperature is raised by a modification of the internal nutritive processes, as in prolonged muscular effort, these changes cannot be suddenly arrested ; and a suppression of the compensative action of the skin is apt to produce disturbances in nutrition, very often resulting in inflammations.

CHAPTER XVI.

MOVEMENTS—VOICE AND SPEECH.

Amorphous contractile substance—Ciliary movements—Movements due to elasticity—Varieties of elastic tissue—Muscular movements—Physiological anatomy of the involuntary muscles—Mode of contraction of the involuntary muscular tissue—Physiological anatomy of the voluntary muscles—Fibrous and adipose tissue in the voluntary muscles—Connective tissue—Blood-vessels and lymphatics of the muscular tissue—Connection of the muscles with the tendons—Chemical composition of the muscles—Physiological properties of the muscles—Muscular contractility, or irritability—Muscular contraction—Changes in the form of the muscular fibres during contraction—*Secousse*, *Zückung*, or spasm—Mechanism of prolonged muscular contraction—Tetanus—Electric phenomena in the muscles—Muscular effort—Passive organs of locomotion—Physiological anatomy of the bones—Marrow of the bones—Medullocells—Myeloplaxes—Periosteum—Physiological anatomy of cartilage—Fibro-cartilage—Voice and speech—Sketch of the physiological anatomy of the vocal organs—Vocal chords—Muscles of the larynx—Mechanism of the production of the voice—Appearance of the glottis during ordinary respiration—Movements of the glottis during phonation—Variations in the quality of the voice, depending upon differences in the size and form of the larynx and the vocal chords—Action of the intrinsic muscles of the larynx in phonation—Action of the accessory vocal organs—Mechanism of the different vocal registers—Mechanism of speech.

The organic, or vegetative functions of animals involve certain movements; and almost all animals possess, in addition, the power of locomotion. Very many of these movements have, of necessity, been considered in connection with the different functions; as the action of the heart and vessels in the circulation, the uses of the muscles in respiration, the ciliary movements in the air-passages, the muscular acts in deglutition, the peristaltic movements, and the mechanism of defæcation and urination. There remain, however, certain general facts with regard to various kinds of movement and the mode of action of the different varieties of muscular tissue, that will demand more or less extended consideration. As regards the exceedingly varied and complex acts concerned in locomotion, it is difficult to fix the limits between anatomy and physiology. A full comprehension of such movements must be preceded by a complete descriptive anatomical account of the passive and active organs of locomotion; and special treatises on anatomy almost invariably give the uses and actions, as well as the structure and relations of these parts.

Amorphous Contractile Substance and Amœboid Movements.—In some of the very lowest orders of beings, in which hardly any thing but amorphous matter and a few granules can be recognized by the microscope, certain movements of elongation and retraction of their amorphous substance have been observed. In the higher animals, similar movements have been noticed in certain of their structures, such as the leucocytes, the contents of the ovum, epithelial cells, and connective-tissue cells. These movements are generally simple changes in the form of the cell, nucleus, or whatever it may be. They are supposed to depend upon an organic principle called sarcode or protoplasm; but it is not known that such movements are characteristic of any one definite proximate principle, nor is it easy to determine their cause and their physiological importance. In the anatomical elements of adult animals of the higher classes, the sarcodic movements usually appear slow and gradual, even when viewed with high magnifying powers; but, in some of the very lowest orders of beings, these movements serve as the means of progression and are more rapid. Such movements are sometimes called amœboid.

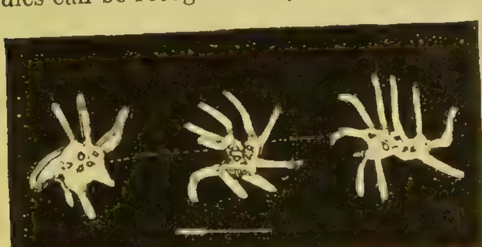


FIG. 146.—*Amœba diffluens, changing in form and moving in the direction indicated by the arrow.* (Longet.)

It does not seem possible, in the present condition of our knowledge, to explain the nature and cause of the movements of homogeneous contractile substance; and it must be excessively difficult, if not impossible, to observe directly the effects of different stimuli, in the manner in which we study the movements of muscles. As far as we can judge, they are analogous to the ciliary movements, the cause of which is equally obscure.

Ciliary Movements.—The epithelium covering certain of the mucous membranes is provided with little hair-like processes upon the free portion of the cells, called cilia. These are in constant motion, from the beginning to the end of life, and they produce currents upon the surfaces of the membranes to which they are attached, the direction being generally from within outward. In many of the infusoria, the ciliary motion serves as a means of progression, effects the introduction of nutriment into the alimentary canal, and, indeed, is almost the sole agent in the performance of the functions involving movement. Even in higher classes, as the mollusca, the movements of the cilia are of great importance. In man and in the warm-blooded animals generally, the ciliated or vibratile epithelium is of the variety called columnar, conoidal, or prismoidal. The cilia are attached to the thick ends of the cells, and they form on the surface of the membrane a continuous sheet of vibrating processes.

It is unnecessary to describe in detail the size and form of the cells provided with cilia, as their variations in different situations have been and will be considered in connection with the physiological anatomy of different parts. In general structure, the ciliary processes are entirely homogeneous, and they gradually taper from their attachment to the cell to an extremity of excessive tenuity. Although anatomists, from time to time, have described striæ at the bases of the cilia and have attempted to explain their motion by a kind of muscular action, no well-defined structure has ever been actually demonstrated in their substance.

The presence of cilia has been demonstrated upon the following surfaces: The respiratory passages, including the nasal fossæ, the pituitary membrane, the summit of the larynx, the bronchial tubes, the superior surface of the velum palati, and the Eustachian tubes; the sinuses about the head; the lachrymal sac and the internal surface of the eyelids; the genital passages of the female, from the middle of the neck of the uterus to the extremities of the Fallopian tubes; and the ventricles of the brain. They probably exist, also, at the neck of the capsule of Müller, in the cortical substance of the kidney. In these situations, to each cell of conoidal epithelium are attached from six to twelve prolongations, about $\frac{1}{25000}$ of an inch in thickness at their base, and from $\frac{1}{5000}$ to $\frac{1}{4000}$ of an inch in length. The appearance of the cilia in detached cells is represented in Fig. 147. When seen *in situ*, they appear regularly disposed upon the surface, are of nearly equal length, and are generally slightly inclined in the direction of the opening of the cavity lined by the membrane.

Fig. 147.—*Ciliated epithelium, from the pituitary membrane.* (Le Bon.)

The ciliary motion is one of the most beautiful physiological demonstrations that can be made with the microscope. By scraping the roof of the mouth of a living frog, the mucous membranes of the respiratory passages in a warm-blooded animal just killed, the beard of the oyster or clam, and placing the preparation, moistened with a little serum, under a magnifying power of about two hundred and fifty diameters, the currents produced in the liquid will be strikingly exhibited. The movements may be studied in detached cells, in the human subject, by introducing a feather into the nose, by which a few cells may be removed with the mucus and can be observed in the same way. This demonstration serves to show the similarity between the movements in man and in the lower orders of animals. When the movements are seen in a large number of cells *in situ*, the appearance is very graphically illustrated by the apt comparison of Henle to the undulations of a field of wheat agitated by the wind. In watching this movement, it is usually seen to gradually diminish in rapidity, until what at first appeared simply as a current, produced by movements too rapid to be studied in detail, becomes revealed as distinct undulations, in which the action of individual cilia can be readily studied. Several kinds of movement have been described, but the most common is a bending of the cilia, simultaneously or in regular succession, in one direction, followed by an undulating return to the perpendicular. The other movements, such as the infundibuliform, in which the point describes a circle around the base, the pendulum-movement, etc., are not common and are unimportant.

The combined action of the cilia upon the surface of a mucous membrane, moving as they do in one direction, is to produce currents of considerable power. This may be illustrated under the microscope by covering the surface with a liquid holding little solid particles in suspension. In this case, the granules are tossed from one portion of the field to another, with considerable force. It is not difficult, indeed, to measure in this way the rapidity of the ciliary currents. In the frog it has been estimated at from $\frac{1}{250}$ to $\frac{1}{175}$ of an inch per second, the number of vibratile movements being from seventy-five to one hundred and fifty per minute. In the fresh-water polyp the movements are more rapid, being from two hundred and fifty to three hundred per minute. There is no reliable estimate of the rapidity of the ciliary currents in man, but they are probably more active than in animals low in the scale.

The movements of cilia, like those observed in fully-developed spermatozoids, seem to be entirely independent of nervous influence, and they are affected only by purely local conditions. They will continue, under favorable circumstances, for more than twenty-four hours after death and can be seen in cells entirely detached from the body when they are moistened with proper fluids. When the cells are moistened with pure water, the activity of the movement is at first increased; but it soon disappears as the cells become swollen. Acids arrest the movement, but it may be excited by feeble alkaline solutions. All abnormal conditions have a tendency either to retard or to abridge the duration of the ciliary motion. It is true that, when the movement is becoming feeble, it may be temporarily restored by very dilute alkaline solutions, but the ordinary stimuli, such as are capable of exciting muscular contraction, are without effect. Purkinje and Valentin, Sharpey, and others, have attempted to excite the movements of cilia by galvanic stimulus, but without success. Anæsthetics and narcotics, which have such a decided effect upon muscular action, have no influence upon the cilia.

It is useless to follow the speculations that have been advanced to account for the movement of cilia. There is no muscular structure in the cilia, no connection with the nervous system, and there seems to be no possibility of explaining the movement except by a bare statement of the fact that the cilia have the property of moving in a certain way so long as they are under normal conditions. As regards the physiological uses of these movements, it is sufficient to refer to the physiology of the parts in which cilia are found, where the peculiarities of their action are considered more in detail. In the lungs and the air-passages generally and in the genital passages of the female, the currents are of considerable importance; but it is difficult to imagine the use of these movements in certain other situations, as the ventricles of the brain.

Movements due to Elasticity.—There are certain important movements in the body that are due simply to the action of elastic ligaments or membranes. These are entirely distinct from muscular movements, and are not even to be classed with the movements produced by the resiliency of muscular tissue, in which that curious property, called muscular tonicity, is more or less involved. Movements of this kind are never excited by nervous, galvanic, or other stimulus, but they consist simply in the return of movable parts to a certain position after they have been displaced by muscular action, and the reaction of tubes after forcible distention, as in the walls of the large arteries.

Elastic Tissue.—Most writers of the present day adopt the division of the elements of elastic tissue into three varieties. This division relates to the size of the fibres; and all varieties are found to possess essentially the same chemical composition and general properties, including the elasticity for which they are so remarkable. On account of the yellow color of this tissue, presenting, as it does, a strong contrast to the white, glistening appearance of the inelastic fibres, it is frequently called the yellow elastic tissue.

The first variety of elastic tissue is composed of small fibres, generally intermingled

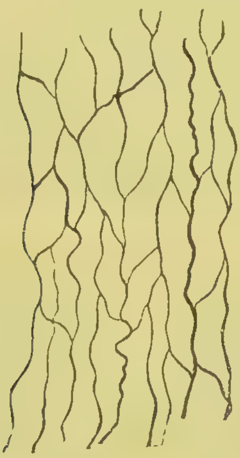


FIG. 148.—*Small elastic fibres, from the peritoneum; magnified* 350 *diameters.* (Kölliker.)

FIG. 149.—*Larger elastic fibres.* (Robin.)

with fibres of the ordinary inelastic tissue. These are sometimes called, by the French, dartoic fibres. They possess all the chemical and physical characters of the larger fibres, but are excessively minute, measuring from $\frac{1}{25000}$ to $\frac{1}{6000}$ or $\frac{1}{5000}$ of an inch in diameter. If we add acetic acid to a preparation of ordinary connective tissue, the inelastic fibres are rendered semitransparent, but the elastic fibres are unaffected and become very distinct. They are then seen isolated, that is, never arranged in bundles, generally with a dark, double contour, branching, brittle, and when broken, their extremities curled and presenting a sharp fracture, like a piece of India-rubber. These fibres pursue a wavy course between the bundles of inelastic fibres in the areolar tissue and in most of the ordinary fibrous membranes, and here they exist as an accessory anatomical element. They are found in greater or less abundance in the situations just mentioned; also, in the ligaments (but not the tendons); in the layers of involuntary muscular tissue; the true skin; the true vocal cords; the trachea, bronchial tubes, and largely in the parenchyma of the lungs; the external layer of the large arteries; and, in brief, in nearly all situations in which the ordinary connective tissue exists.

The second variety of elastic tissue is composed of fibres, larger than the first, ribbon-shaped, with well-defined outlines, anastomosing, undulating or curved in the form of the letter S, presenting the same curled ends and sharp fracture as the smaller fibres. These measure from $\frac{1}{5000}$ to $\frac{1}{3000}$ of an inch in diameter. Their type is found in the ligamenta subflava and the ligamentum nuchæ. They are also found in some of the ligaments of the larynx, the stylo-hyoid ligament, and the suspensory ligament of the penis. The form and arrangement of these fibres may be very strikingly demonstrated by tearing off a portion of the ligamentum nuchæ and lacerating it with needles in a drop of acetic acid. The action of the acetic acid renders the accessory structures of the ligament transparent, and the elastic fibres become very distinct. The same may be accomplished by boiling the tissue for a short time in caustic soda.

The third variety of elastic tissue can hardly be said to consist of fibres, as their branches are so short and their anastomoses so frequent. This kind of structure is found forming the middle coat of the large arteries, and it has already been described in connection with the vascular system. The fibres are very large, flat, with numerous short branches, "which unite again with the trunk from which they originate or with adjacent fibres. In certain situations, the interstices are considerable, in proportion to the diameter of the fibres, and the anastomosing branches are given off at acute angles, so that they follow pretty closely the direction of the trunks, and the anastomoses do not disturb the longitudinal direction and parallelism of the fibres. Indeed, the anastomoses are so numerous, and the intervals so small, proportionally to the fibres, that we should believe we had under observation a reticulated membrane, presenting openings, rounded and oval, some large and others small." (Henle.) These anastomosing fibres, forming the so-called fenestrated membranes, are arranged in layers, and the structure is sometimes called the lamellar elastic tissue.

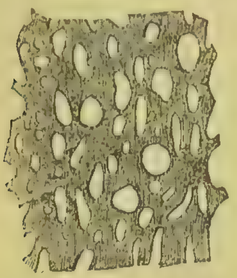


Fig. 150.—*Large elastic fibres (fenestrated membrane), from the middle coat of the carotid of the horse; magnified* 350 *diameters.* (Kölliker.)

The great resistance which the elastic tissue presents to chemical action serves to distinguish it from nearly every other structure in the body. We have already seen that it is not affected by acetic acid or by boiling with caustic soda. It is not softened by prolonged boiling in water, but it is slowly dissolved, without decomposition, by sulphuric, nitric, or hydrochloric acid, the solution not being precipitable by potash. Its organic base is a nitrogenized substance called elasticine, containing carbon, hydrogen, oxygen, and nitrogen, without sulphur. This is supposed to be identical with the sarcolemma of the muscular tissue.

The purely physical property of elasticity plays an important part in many of the animal functions. We have already had an example of this in the action of the large arteries in the circulation and in the resiliency of the parenchyma of the lungs; and we shall have occasion, in treating of the functions of other parts, to refer again to the uses of elastic membranes and ligaments. The ligamenta subflava and the ligamentum nuchæ are important in aiding to maintain the erect position of the body and head, and to restore this position when flexion has been produced by muscular action. Still, the contraction of muscles is also necessary to keep the body in a vertical position.

Muscular Movements.

Muscular movements are observed only in the higher classes of animals. Low in the scale of animal life, we have the contractions of amorphous substance and ciliary motion; and, in some vegetables, movements, even attended with locomotion, have been observed. These facts make the absolute distinction between the two kingdoms a question of some difficulty; but in animals only, do we have a distinct muscular system.

The muscular movements capable of being excited by stimulus of various kinds are divided into voluntary and involuntary; and generally there is a corresponding division of the muscles as regards their minute anatomy. The latter, however, is not absolute; for there are certain involuntary functions, like the action of the heart or the movements of deglutition, that require the rapid, vigorous contraction characteristic of the voluntary muscular tissue, and here we do not find the structure characteristic of the involuntary muscles. With a few exceptions, however, the anatomical division of the muscular tissue into voluntary and involuntary is sufficiently distinct.

Physiological Anatomy of the Involuntary Muscles.—We have so often described this tissue, as it is found in the vascular system, the digestive organs, the skin, and in other situations, that it will not be necessary, in this connection, to give more than a sketch of its structure and mode of action.

The involuntary muscular system presents a striking contrast to the voluntary muscles, not only in its minute anatomy and mode of action, but in the arrangement of its fibres. While the voluntary muscles are almost invariably attached by their two extremities to movable parts, the involuntary muscles form sheets or membranes in the walls of hollow organs, and, by their contraction, they simply modify the capacity of the cavities which they enclose. Various names have been given to this tissue to denote its distribution, mode of action, or structure. The name involuntary muscle indicates that its contraction is not under the control of the will; and this is the fact, these muscles being chiefly animated by the sympathetic system of nerves, while the voluntary muscles are supplied mainly from the cerebro-spinal system. On account of the peculiar structure of these fibres, they have been called muscular fibre-cells, smooth muscular fibres, pale fibres, non-striated fibres, fusiform fibres, and contractile cells. The distribution of these fibres to parts concerned in the organic or vegetative functions, as the alimentary canal, has given them the name of organic muscular fibres, or fibres of organic, or vegetative life. It is difficult to isolate the individual fibres of this tissue in microscopical preparations; and, when seen *in situ*, their borders are faint, and we can make out their arrangement

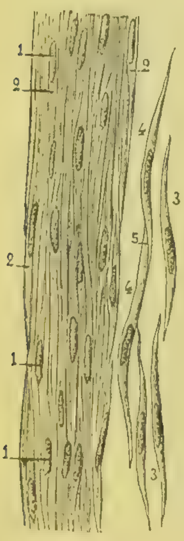


FIG. 151.—*Muscular fibres from the urinary bladder of the human subject; magnified 200 diameters.* (Sappey.)

1, 1, 1, nuclei; 2, 2, 2, borders of some of the fibres; 3, 3, isolated fibres; 4, 4, two fibres joined together at (5).

FIG. 152.—*Muscular fibres from the aorta of the calf; magnified 200 diameters.* (Sappey.)

1, 1, fibres joined with each other; 2, 2, 2, isolated fibres.

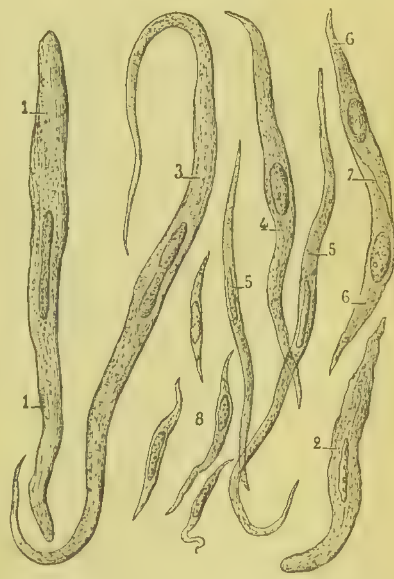


FIG. 153.—*Muscular fibres from the uterus of a woman who died at the ninth month of utero-gestation; magnified 350 diameters.* (Sappey.)

1, 1, 2, short, wide fibres; 3, 4, 5, 5, longer and narrower fibres; 6, 6, two fibres united at (7); 8, small fibres in process of development.

best by the appearance of their nuclei. Robin recommends soaking of the tissue for a few days in a mixture of one part of ordinary nitric acid to ten of water. This renders the fibres dark and granular, makes their borders very distinct, and frequently some of them become entirely isolated. The nuclei, however, are obscured. In their natural condition, the fibres are excessively pale, very finely granular, flattened, and of an elongated spindle-shape, with a very long, narrow, almost linear nucleus in the centre. The nucleus generally has no nucleolus, and it is sometimes curved or shaped like the letter S.

The ordinary length of these fibres is about $\frac{1}{500}$, and their breadth about $\frac{1}{4000}$ of an inch. In the gravid uterus they undergo remarkable hypertrophy, measuring here from $\frac{1}{80}$ to $\frac{1}{50}$ of an inch in length, and $\frac{1}{2000}$ of an inch in breadth. The peculiarities of their structure in the uterus will be fully considered under the head of generation.

In the contractile sheets formed of involuntary muscular tissue, the fibres are arranged side by side, are closely adherent, and their extremities are, as it were, dove-tailed into each other. Generally the borders of the fibres are regular and their extremities are simple; but sometimes the ends are forked, and the borders present one or more little projections. It is very seldom that we see the fibres in a single layer, except in the very smallest arterioles. Usually the layers are multiple, being superimposed in regular order. The action of acetic acid is to render the fibres pale, so that their outlines become almost indistinguishable, and to bring out the nuclei more strongly. If we have an indistinct sheet of this tissue in the field of view, the addition of acetic acid, by bringing out the long, narrow, and curved nuclei arranged in regular order, and by rendering the fibrous and other structures more transparent, will often enable us to recognize its character.

Contraction of the Involuntary Muscular Tissue.—The mode of contraction of the involuntary muscles is peculiar. It does not take place immediately upon the reception of a stimulus, applied either directly or through the nerves, but it is gradual, enduring for a time and then followed by slow and gradual relaxation. A description of the peristaltic movements of the intestines gives a perfect idea of the mode of contraction of these fibres, with the gradual propagation of the stimulus along the alimentary canal, as the food makes its impression upon the mucous membrane. An equally striking illustration is afforded by labor-pains. These are due to the muscular contractions of the uterus, and they last from a few seconds to one or two minutes. Their gradual access, continuation for a certain period, and gradual disappearance coincide exactly with the history of the contractions of the involuntary muscular fibres.

The contraction of the involuntary muscular tissue is slow, and the fibres return slowly to a condition of repose. The movements are always involuntary. Peristaltic action is the rule, and the contraction takes place progressively and without oscillations. Contractility persists for a long time after death. Arrest of function is followed by little or no atrophy, and hypertrophy is very marked as the result of exaggerated action. Excitation of the nerves has less influence upon contraction of these fibres than direct excitation of the muscles. The involuntary muscular tissue is regenerated very rapidly, while the structure of the voluntary muscles is restored with great difficulty after destruction or division. (Legros and Onimus.)

Physiological Anatomy of the Voluntary Muscles.[1]—A voluntary muscle is the most highly organized and is possessed of the most varied endowments of all living structures. It contains, in addition to its own peculiar contractile substance, fibres of inelastic and elastic tissue, adipose tissue, numerous blood-vessels, nerves, and lymphatics, with certain nuclear and cellular anatomical elements. The muscular system constitutes by far the greatest part of the organism, and its nutrition consumes a large proportion of the reparative material of the blood, while its disassimilation furnishes a corresponding quantity of excrementitious matter. The condition of the muscular system, indeed, is an almost unfailing evidence of the general state of the body, allowing, of course, for peculiarities in different individuals. Among the characteristic properties of the muscles are, elasticity, a constant and insensible tendency to contraction, called tonicity, the power of contracting forcibly on the reception of a proper stimulus, called irritability, a peculiar kind of sensibility, and the faculty of generating galvanic currents. The relations of particular muscles, as taught by descriptive anatomy, involve special functions; but the most interesting physiological points connected with this system relate to the general properties and functions of the muscles, and must necessarily be prefaced with a sketch of their general anatomy.

It has been demonstrated by minute dissection that all of the red, or voluntary muscles are made up of a great number of microscopic fibres, known as the primitive muscular fasciculi. These are called red, striated, or voluntary fibres, or the fibres of animal life. Their structure is complex, and they may be subdivided longitudinally into fibrillæ, and transversely into disks, so that it is somewhat doubtful as to what is, strictly speaking, the ultimate anatomical element of the muscular tissue.

A primitive muscular fasciculus runs the entire length of the muscle, and is enclosed in its own sheath, without branching or inosculation. This sheath contains the true muscular substance only, and it is not penetrated by blood-vessels, nerves, or lymphatics. If we examine with the microscope a thin, transverse section of a muscle, the divided ends of the fibres will present an irregularly polygonal form, with rounded corners. They seem to be cylindrical, however, when viewed in their length and isolated. Their color by transmitted light is a delicate amber, resembling somewhat the color of the blood-corpuscles.

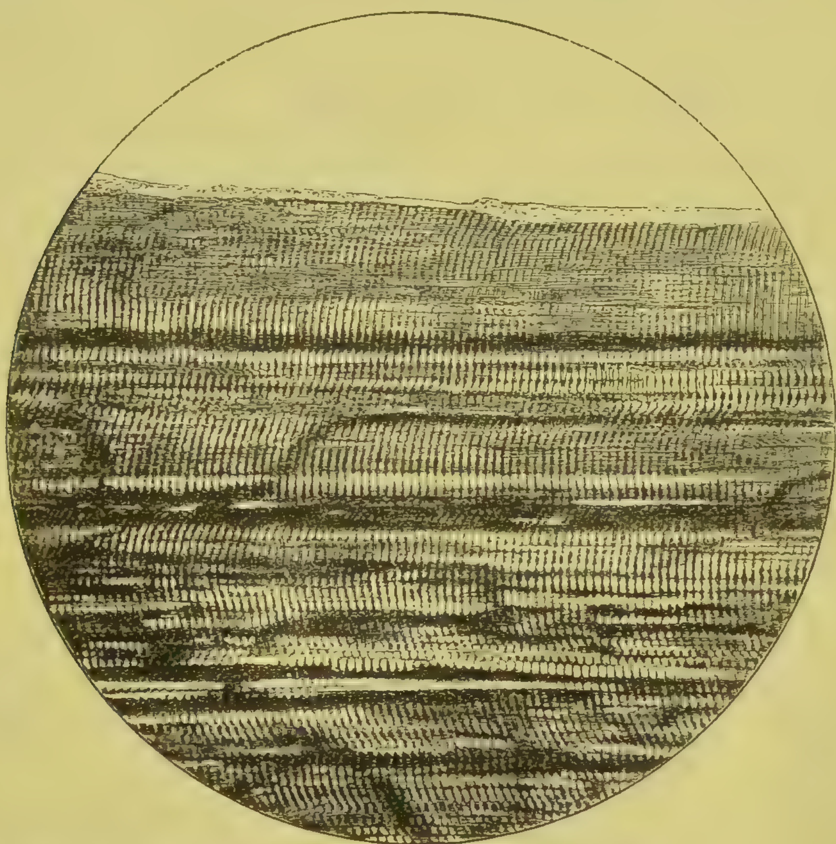


FIG. 154.—*Striated muscular fibres, from the mouse; magnified 500 diameters.* (From a photograph taken at the United States Army Medical Museum.)
The injected capillaries are seen, somewhat out of focus.

The primitive fasciculi vary very much in size in different individuals, in the same individual under different conditions, and in different muscles. As a rule, they are smaller in young persons and in females than in adult males. They are comparatively small in persons of slight muscular development. In persons of great muscular vigor, or when the general muscular system or particular muscles have been increased in size and power by exercise, the fasciculi are relatively larger. It is probable that the physiological increase in the size of a muscle from exercise is due to an increase in the size of the pre-existing fasciculi, and not to the formation of any new elements. In young persons, the fasciculi are from $\frac{1}{1700}$ to $\frac{1}{1200}$ of an inch in diameter. In the adult, they measure from $\frac{1}{450}$ to $\frac{1}{250}$ of an inch.

The appearance of the primitive muscular fasciculi under the microscope is characteristic and unmistakable. They present regular, transverse striæ, formed of alternating dark and clear bands about $\frac{1}{25000}$ of an inch wide. These are generally very distinct in healthy muscles. In addition, we frequently observe longitudinal striæ, not so distinct, and quite difficult to follow to any extent in the length of the fasciculus, but tolerably well marked, particularly in muscles that are habitually exercised. The muscular substance, presenting this peculiar striated appearance, is enclosed in an excessively thin but elastic and resisting tubular membrane, called the sarcolemma or myolemma, which is probably composed of the same substance as the elastic tissue. This envelope cannot be seen in ordinary preparations of the muscular tissue; but it frequently happens that the contractile muscular substance is broken, leaving the sarcolemma intact, which gives a good view of the membrane and conveys an idea of its strength and elasticity. Attached to the inner surface of the sarcolemma, are numerous small, elongated nuclei with their long diameter in the direction of the fasciculi. These are usually not well seen in the unaltered muscle, but the addition of acetic acid renders the muscular substance pale and destroys the striæ, when the nuclei become very distinct.

Water, after a time, acts upon the muscular tissue, rendering the fasciculi somewhat paler and larger. Acetic acid and alkaline solutions efface the striæ, and the fibres become semitransparent. In fasciculi that are slightly decomposed, there is frequently a separation at the extremity into numerous smaller fibres, called fibrillæ. These, when isolated, present the same striated appearance as the primitive fasciculus; viz., alternate dark and light portions. They measure about $\frac{1}{25000}$ of an inch in diameter, and their number, in the largest primitive fibres, is estimated by Kölliker at about two thousand. The structure of the fibrillæ is probably uniform, the appearance of alternate dark and light segments being due to differences in thickness. In fact, it is well known that water, by its simple mechanical action, swells the fibrillæ and causes the striæ to disappear.

Late researches have shown that the interior of each primitive fasciculus is penetrated by an excessively delicate membrane, closely surrounding the fibrillæ. This arrangement may be distinctly seen in a thin section of a fibre treated with a solution of salt in water in the proportion of five parts per thousand. The arrangement of this membrane, which is nothing more nor less than a series of tubular sheaths for the fibrillæ, is a strong argument in favor of the view that the fibrilla is the anatomical element of the muscular tissue.

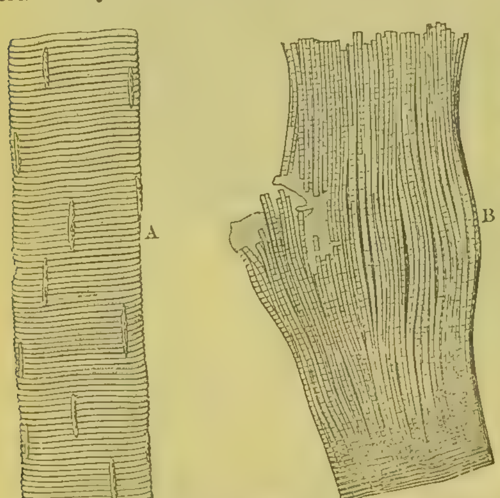


FIG. 155.—*Voluntary muscular fibres; magnified 250 diameters.* (Sappey.)
A, transverse striæ and nuclei of a primitive fasciculus; B, longitudinal striæ and fibrillæ of a primitive fasciculus in which the sarcolemma has been lacerated at one point by pressure.

When we come to the question of the real anatomical element of the muscular tissue, there are only two reasonable views that present themselves. One is that any subdivision of the primitive fasciculus is artificial, and that it, with its investing membrane, the sarcolemma, is the true element. An argument in favor of this opinion is that the tissue is most readily separated into fasciculi, each enclosed in its own membrane and not penetrated by vessels, nerves, or lymphatics; while the fibrillæ are situated in a reticulum of canals, from which they cannot readily be isolated. The other opinion, that the fibrillæ are the ultimate elements, is based upon the fact that these little fibres present the striæ and all the anatomical characteristics of the primitive fasciculi, and that by far the most natural and easy mode of separation of these fasciculi is in a longitudinal direction. The question of adopting one or the other of these views is not of very great physiological importance.

Fibrous and Adipose Tissue in the Voluntary Muscles.—The structure of the muscles strikingly illustrates the relations between the principal and the accessory anatomical elements of tissues. The characteristic, or principal element is, of course, the muscular fibre or fibrilla; but we also find in the substance of the muscles certain anatomical elements, not peculiar to the muscles, and merely accessory in their function, but none the less necessary to their proper constitution. For example, every muscle is composed of a number of primitive fasciculi; but these are gathered into secondary bundles, which in turn are collected into bundles of greater and greater size, until, finally, the whole muscle is enveloped in its sheath and is penetrated by a fibrous connective substance. We find, probably, in the muscles, the best illustration of the structure of what is known as the connective tissue.

Connective Tissue.—We have already had occasion to refer to certain of the elements of connective tissue, more especially the inelastic and elastic fibres. In this connection, we shall treat specially of the connective tissue of the muscles; but our description will answer for almost all situations in which fibrous tissue exists merely for the purpose of holding parts together. In the muscles, we have a membrane holding a number of the primitive fasciculi into secondary bundles. This is known as the perimysium. The fibrous membranes that connect together these secondary bundles with their contents are enclosed in a sheath enveloping the whole muscle, sometimes called the external perimysium. The peculiarity of these membranes, and their distinction from the sarcolemma, are that they have a fibrous structure and are connected together throughout the muscle, while the tubes forming the sarcolemma are structureless, and each one is distinct.

FIG. 156.—*Fibres of tendon of the human subject.* (Rollett.)

The name now most generally adopted for the tissue under consideration is connective tissue. It has been called cellular, areolar, or fibrous, but most of these names were given to it without a clear idea of its structure. Its principal anatomical element is a fibre of excessive, almost immeasurable, tenuity, wavy, and with a single contour. These fibres are connected into bundles of very variable size and are held together by an adhesive amorphous substance. The wavy lines that mark the bundles of fibres give them a very characteristic appearance.

The direction and arrangement of the fibres in the various tissues present marked differences. In the loose areolar tissue beneath the skin and between the muscles, and in the loose structure surrounding some of the glands and connecting the sheaths of blood-vessels and nerves to the adjacent parts, the bundles of fibres form a large net-work and are very wavy in their course. In the strong, dense membranes, as the aponeuroses, the proper coats of many glands, the periosteum and perichondrium, and the serous membranes, the waves of the fibres are shorter, and the fibres themselves interlace much more closely. In the ligaments and tendons, the fibres are more nearly straight and are all arranged longitudinally.

On the addition of acetic acid, the bundles of inelastic fibres swell up, become semi-transparent, and the nuclei and elastic fibres are brought out. The proportion of elastic fibres differs very much in different situations, but they are all of the smallest variety, and they present a striking contrast to the inelastic fibres in their form and size. Although they are still very small, they always present a double contour.

Fig. 157.—*Loose net-work of connective tissue from the human subject, showing the fibres and cells.* (Rollett.) *a*, *a*, a capillary blood-vessel.

Certain cellular and nuclear elements are always found in the connective tissue. The cells have been described under the name of connective-tissue cells. They are very irregular in size and form, some of them being spindle-shaped or caudate, and others, star-shaped. They possess one, and sometimes two or three clear, ovoid nuclei, with distinct nucleoli. On the addition of acetic acid the cells disappear, but the nuclei are unaffected. These are the fibro-plastic elements of Lebert, and the embryo-plastic elements of Robin. It is impossible to give any accurate measurements of the cells, on account of their great variations in size. The length of the nuclei is from $\frac{1}{3600}$ to $\frac{1}{2500}$ of an inch, and their diameter, from $\frac{1}{5000}$ to $\frac{1}{4000}$ of an inch. The appearance of the connective tissue, with a few cells and nuclei, is represented in Fig. 157.

Between the muscles, and in the substance of the muscles between the bundles of fibres, there always exists a greater or less quantity of adipose tissue in the meshes of the fibrous structure.

Blood-vessels and Lymphatics.—The muscles are abundantly supplied with blood-vessels, generally by a number of small arteries with two satellite veins. The capillary arrangement in this tissue is peculiar. From the smallest arterioles, capillary vessels are given off, arranged in a net-work with tolerably regular, oblong, rectangular meshes, their long diameter following the direction of the fibres. These envelop each primitive fasciculus, enclosing it completely, the artery and vein being upon the same side. The capillaries are smaller than in any other part of the vascular system. When distended with blood they are from $\frac{1}{4500}$ to $\frac{1}{3750}$ of an inch in diameter; and when empty their diameter is from $\frac{1}{7000}$ to $\frac{1}{5500}$ of an inch.

The arrangement of the lymphatics in the muscles has never been definitely ascertained. There are numerous lymphatics surrounding the large vascular trunks of the extremities and of the abdominal and thoracic walls, which, it would appear, must come from the substance of the muscles; but they have never been traced to their origin. Sappey has succeeded in injecting lymphatics upon the surface of some of the larger muscles, but he has not been able to follow them into the muscular substance.

Connection of the Muscles with the Tendons.—It is now generally admitted that the primitive muscular fasciculi terminate in little conical extremities, which are received into corresponding depressions in the bundles of fibres composing the tendons; but this union is so close, that the muscle or the tendon may be ruptured without a separation at the point of union. In the penniform muscles this arrangement is quite uniform and elegant. In other muscles it is essentially the same, but the perimysium seems to be continuous with the loose areolar tissue enveloping the corresponding tendinous bundles.

Chemical Composition of the Muscles.—We are as yet so little acquainted with the exact constitution of the nitrogenized constituents of the body, that we cannot appreciate the nature of all the proximate principles that exist in the muscular substance. The most important of these is musculine. This resembles fibrin, but it presents certain points of difference in its behavior to reagents, by which it may be readily distinguished. One of its peculiar properties is that it is dissolved at an ordinary temperature by a mixture of one part of hydrochloric acid and ten of water.

The muscular substance is permeated by a fluid, called the muscular juice, which contains a peculiar coagulable principle called myosine.

Combined with the organic principles, we find a great variety of mineral salts in the muscular substance, that cannot be separated without incineration. Certain excrementitious matters have also been found in the muscles; and probably nearly all of those eliminated by the kidneys exist here, although they are taken up by the blood as fast as they are produced and are consequently detected with difficulty. The muscles also contain inosite, inosic acid, lactic acid, and certain other acids of fatty origin. During life, the muscular fluid is slightly alkaline, but it becomes acid soon after death. The muscle itself, during contraction, has an acid reaction. The muscular juice is alkaline or neutral after moderate exercise, as well as during complete repose; but, when a muscle is made to undergo excessive exercise, the lactic acid exists in greater quantity, and the reaction becomes acid.

Physiological Properties of the Muscles.

The general properties of the striated muscles, as distinguished from all other tissues except the involuntary muscles, are as follows: 1. Elasticity; 2. Tonicity; 3. Sensibility of a peculiar kind; 4. Contractility, or irritability. These are all necessary to the physiological action of the muscles. Their elasticity is brought into play in opposing muscles or sets of muscles; one set acting to move a part and to extend the antagonistic muscles, which, by virtue of their elasticity, retract when the extending force is removed. Their tonicity is an insensible and a more or less constant contraction, by which the action of opposing muscles is balanced when both are in the condition of what we call repose. Their sensibility is peculiar and is expressed chiefly in the sense of fatigue and in the appreciation of weight and of resistance to contraction. Their contractility or irritability is the property which enables them to contract and exert a certain amount of mechanical force under the proper stimulus. All of these general properties strictly belong to physiology, as do some special acts that are not necessarily involved in the study of ordinary descriptive anatomy.

Elasticity of Muscles.—The true muscular substance contained in the sarcolemma is eminently contractile; and, although it may possess a certain degree of elasticity, this property is most strongly marked in the accessory anatomical elements. The interstitial fibrous tissue is loose and possesses a certain number of elastic fibres, and, as we have seen, the sarcolemma is very elastic. It is probably the sarcolemma that gives to the muscles their retractile power after simple extension.

It is unnecessary to follow out in detail all of the numerous experiments that have been made upon the elasticity of muscles. There is a certain limit, of course, to their perfect elasticity (understanding by this the degree of extension that is followed by complete retraction), and this cannot be exceeded in the human subject without dislocation of parts. It has been found by Marey, that the gastrocnemius muscle of a frog, detached from the body, can be extended about one-fiftieth of an inch by a weight of a little more than three hundred grains. This weight, however, did not extend the muscle beyond the limit of perfect elasticity. The muscle of a frog of ordinary size was extended beyond the possibility of complete restoration, by a weight of about seven hundred and fifty grains. Marey also showed that fatigue of the muscles increased their extensibility and diminished their power of subsequent retraction. This fact has an application to the physiological action of muscles; for it is well known that they are unusually relaxed during fatigue after excessive exertion, and, as we should expect, they are at that time more than ordinarily extensible.

Muscular Tonicity.—The muscles, under normal conditions, have an insensible and a constant tendency to contract, which is more or less dependent upon the action of the motor nerves. If, for example, a muscle be cut across in a surgical operation, the divided extremities become permanently retracted; or, if the muscles of one side of the face be paralyzed, the muscles upon the opposite side insensibly distort the features. It is difficult to explain these phenomena by assuming that tonicity is due to reflex action, for there is no evidence that the contraction takes place as the consequence of a stimulus. All that we can say is, that a muscle, not excessively fatigued, and with its nervous connections intact, is constantly in a state of insensible contraction, more or less marked, and that this is an inherent property of all of the contractile tissues.

Sensibility of the Muscles.—The muscles possess to an eminent degree that kind of sensibility which enables us to appreciate the power of resistance, immobility, and elasticity of substances that are grasped, on which we tread, or which, by their weight, are opposed to the exertion of muscular power. It is by the appreciation of weight and resistance that we regulate the amount of force required to accomplish muscular acts. These properties refer chiefly to simple muscular efforts. After long-continued exertion we appreciate a sense of fatigue that is peculiar to the muscles. It is difficult to separate this entirely from the sense of nervous exhaustion, but it seems to be, to a certain extent, distinct; for, when suffering from the fatigue that follows over-exertion, it seems as though we could send a nervous stimulus to the muscles, to which they are, for the time, unable to respond. When we come to consider fully the subjects of muscular and nervous irritability, we shall see that these two properties are entirely distinct, and that we may exhaust or destroy the one without necessarily affecting the other.

When the muscles are thrown into spasm or tetanic contraction, a peculiar sensation is produced, entirely different from painful impressions made upon the ordinary sensitive nerves. In the cramps of cholera, tetanus, or the convulsions from strychnine, these distressing sensations are very marked. The so-called recurrent sensibility of the anterior roots of the spinal nerves is probably due in part to the tetanic contractions produced by galvanizing these filaments. This question, however, will be taken up again in connection with the nervous system.

If the muscles possess any general sensibility, it is very faint. A muscle may be lacerated or irritated in any way without producing actual pain, although we always can appreciate the contraction produced by irritants and the sense of tension when the muscles are drawn upon.

Muscular Contractility, or Irritability.—Physiologists now regard muscular irritability as synonymous with contractility; and, perhaps, the latter term more nearly expresses the fact, although the term irritability, applied to the nerves, and even of late years to the glands, is one very generally used.

By irritability we understand a property belonging to highly-organized parts, which enables them to perform certain peculiar and characteristic functions in obedience to a proper stimulus. In the sense in which the term is generally received, it is proper to apply it to any tissue or organ that performs its vital function, so called, under a natural or an artificial stimulus. The nerves receive impressions and carry a stimulus to the muscles, causing them to contract. This property, which is always present during life, under normal conditions, and which persists for a certain period after death, is called nervous irritability. It has lately been shown that the application of a proper stimulus will induce secretion by the glands; and Bernard has called this glandular irritability. The application of a stimulus to the muscular tissue causes the fibres to contract; and this is muscular irritability. As it always involves contraction and is extinct only when the muscles can no longer act, it is equally proper to call this property contractility. No property, such as we understand by this definition of irritability, is manifested by tissues or organs that have purely passive or mechanical functions, such as bones, cartilages, and fibrous or elastic membranes. The term irritability can only be applied properly to nerves or nerve-centres, to contractile structures, and to glands.

During life and under normal conditions, the muscles will always contract in obedience to a proper stimulus applied either directly or through the nerves. In the natural action of the organism, this contraction is induced by nervous influence through reflex action or volition. Still, a muscle may be living and yet have lost its contractility. For example, after a muscle has been for a long time paralyzed and disused, the application of the most powerful galvanic excitation will fail to induce contraction. But, when we examine such a muscle with the microscope, it is found that the nutrition has become profoundly affected, and that the contractile substance has disappeared, giving place to inert fatty matter. Muscular contractility persists for a certain time after death and in muscles separated from the body; and this fact has been taken advantage of by physiologists in the study of the so-called vital properties of the muscular tissue. We have already seen that a muscle detached from the living body continues for a time to respire, and probably it undergoes some of the changes of disassimilation observed in the organism. So long as these changes are restricted to the limits of physical and chemical integrity of the fibre, contractility remains. As these processes are very slow in the cold-blooded animals, the irritability of all the parts persists for a considerable time after death. We have repeatedly demonstrated muscular contractility, several days after death, in alligators and turtles.

In the human subject and the warm-blooded animals, the muscles cease to respond to excitation a few hours after death, although the time of disappearance of irritability is very variable. Nysten, in a number of experiments upon the disappearance of contractility in the human subject after decapitation, found that different parts lost their contractility at different periods, but that generally this depended upon exposure to the air.

With the exception of the right auricle of the heart, the muscles of the voluntary system were the last to lose their irritability. In one instance, certain of the voluntary muscles that had not been exposed retained their contractility seven hours and fifty minutes after death. The observations of Longet and Masson show that a galvanic shock, sufficiently powerful to produce death, instantly destroys the irritability of the muscular tissue and of the motor nerves.

One of the most important questions to determine with regard to muscular irritability is whether it be a property inherent in the muscular tissue or derived from the nervous system. The fact that muscles can be excited to more powerful and regular contractions by stimulating the motor nerves than by operating directly upon their substance, and the great difficulty in tracing the nerves to their termination in the muscles, have led to the view that muscular contractility is dependent upon nervous influence, and consequently that the muscles have no irritability or contractility, as a property inherent in their own substance. This doctrine, however, cannot be sustained.

The experiments of Longet, published in 1841, presented almost conclusive proof of the independence of muscular irritability. He resected the facial nerve and found that it ceased to respond to mechanical and galvanic stimulus, or, in other words, lost its irritability, after the fourth day. Operating, however, upon the muscles supplied exclusively with filaments from this nerve, he found that they responded promptly to mechanical and galvanic irritation, and that they continued to contract, under stimulation, for more than twelve weeks. In some farther experiments it was shown that, while the contractility of the muscles could be seriously influenced through the nervous system, this was effected only by modifications in their nutrition. When the mixed nerves were divided, the nutrition of the muscles was generally disturbed; and, although muscular irritability persisted for some time after the nervous irritability had disappeared, it became very much diminished at the end of six weeks. These experiments are very striking and satisfactory; but the whole question was definitively settled by the observations of Bernard upon the peculiar influence of the woorara-poison and the sulphocyanide of potassium. As the result of these experiments, it was ascertained that some varieties of woorara destroy the irritability of the motor nerves, leaving the sensitive filaments intact. If a frog be poisoned by introducing a little of this agent under the skin, irritation, galvanic or mechanical, applied to an exposed nerve, fails to produce the slightest muscular contraction; but, if the stimulus be applied directly to the muscles, they will contract vigorously. In this way the nerves are, as it were, dissected out from the muscles; and the discovery of an agent that will paralyze the nerves without affecting the muscles affords conclusive proof that the irritability of these two systems is entirely distinct. If a frog be poisoned with sulphocyanide of potassium, precisely the contrary effect will be observed; that is, the muscles will become insensible to excitation, while the nervous system is unaffected. This fact may be demonstrated by applying a tight ligature around the body in the lumbar region, involving all the parts except the lumbar nerves. If the poison be now introduced beneath the skin of the parts above the ligature, the anterior parts only are affected, because the vascular communication with the posterior extremities is cut off. If the

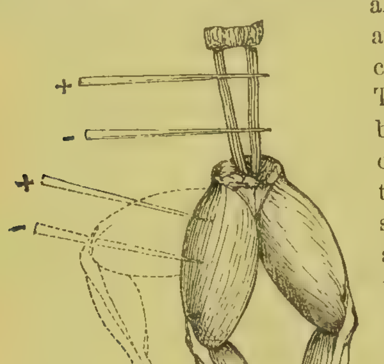


FIG. 158.—*Frog's legs prepared so as to show the effects of woorara.* (Bernard.) Galvanization of the nerves in this animal, which has been poisoned with woorara, has no effect; while galvanization applied directly to the muscles (see dotted lines) produces contraction.

exposed nerves be now galvanized, the muscles of the legs are thrown into contraction, showing that the nervous irritability remains. Reflex movements in the posterior extremities may also be produced by irritation of the parts above the ligature. These experiments, most of which we have frequently repeated, taken in connection with the observations of Longet, leave no doubt of the existence of an inherent and independent irritability in the muscular tissue. Contractions of muscles, it is true, are normally excited through the nervous system, and artificial stimulation of a motor or mixed nerve is the most efficient method of producing the simultaneous action of all the fibres of a muscle or of a set of muscles; but galvanic, mechanical, or chemical irritation of the muscles themselves will produce contraction, after the nervous irritability has been abolished.

The conditions under which muscular irritability exists are simply those of normal nutrition of the muscular tissue. When the muscles have become profoundly affected in their nutrition, as the result of section of the mixed nerves or after prolonged paralysis, the irritability disappears and cannot be restored. The determination of the presence or absence of muscular contractility, in cases of paralysis, is one of the methods of ascertaining whether treatment directed to the restoration of the nervous power will be likely to be followed by favorable results. If the muscular irritability have entirely disappeared, it is almost useless to attempt to restore the functions of the part.

A great many experiments have been made with regard to the influence of the circulation upon muscular irritability, chiefly with reference to the effects of tying large vessels. Among the most recent are those of Longet. He tied the abdominal aorta in five dogs and found that voluntary motion ceased in about a quarter of an hour, and that the muscular irritability was extinct in two hours and a quarter. When the blood was restored, after three or four hours, by removing the ligature, the irritability and finally voluntary movement returned. These experiments show that the circulation of the blood is necessary to the contractility of the muscles. Tying the vena cava did not affect the irritability of the muscles. In dogs in which this experiment was performed, the lower extremities preserved their contractility, and the voluntary movements were unaffected up to the time of death, which took place in twenty-six hours.

The relations of muscular irritability to the circulation have been farther illustrated, in some very curious and interesting experiments, by Dr. Brown-Séquard. The first observations were made upon two men executed by decapitation. Thirteen hours and ten minutes after death, when the muscular irritability had entirely disappeared and was succeeded by cadaveric rigidity, a quantity of fresh, defibrinated venous blood, from the human subject, was injected into the arteries of one hand and was returned by the veins. It was afterward reinjected several times during a period of thirty-five minutes. The whole time occupied in the different injections was from ten to fifteen minutes. Ten minutes after the last injection, and about fourteen hours after death, the irritability was found to have returned, in a marked degree, in twelve muscles of the hand. There were only two muscles out of the nineteen, in which the irritability could not be demonstrated. Three hours after, the irritability still existed, but it disappeared a quarter of an hour later. The second observation was essentially the same, except that defibrinated blood from the dog was used, and the experiments were made upon the muscles of the arm. The irritability was restored in all of the muscles, and it persisted, the cadaveric rigidity having disappeared, twenty hours after decapitation. These experiments are exceedingly interesting, as showing the dependence of irritability upon certain of the processes of nutrition, which are probably restored, though temporarily and imperfectly, by the injection of fresh blood. They are also important in connection with the study of cadaveric rigidity of muscles, a condition which follows the loss of their so-called vital properties. The subject of cadaveric rigidity will be fully discussed as one of the phenomena of death.

Muscular Contraction.

The stimulus of the will, conveyed through the conductors of motor influences from the brain to a muscle or set of muscles, produces an impression upon the muscular fibres and causes them to contract. In parts where the muscles have been exercised and educated, this action is regulated with exquisite nicety, so that the most delicate and rapid, as well as powerful contractions may be produced. Certain movements, not under the control of the will, are produced as the result of unconscious reflection from a nervous centre, along the motor conductors, of an impression made upon sensitive nerves. During this action, certain important phenomena are observed in the muscles themselves. They change in form, consistence, and, to a certain extent, in their constitution; the different periods of their stimulation, contraction, and relaxation are positive and well-marked; their nutrition is for the time modified; they develop galvanic currents; and, in short, they present a number of general phenomena, distinct from the results of their action, that are more or less interesting and important to the physiologist.

The most striking of the phenomena accompanying muscular action is shortening and hardening of the fibres. It is only necessary to observe the action of any well-developed muscle to appreciate these changes. The active shortening is shown by the approximation of the points of attachment, and the hardening is sufficiently palpable. The latter phenomenon is marked in proportion to the development of the true muscular tissue and its freedom from inert matter, such as fat. We have already seen that it is the muscular substance alone which has the property of contraction; and we have shown that this action increases the consumption of oxygen and probably of other matters, the production of carbonic acid and some other excrementitious principles, and that it develops heat.

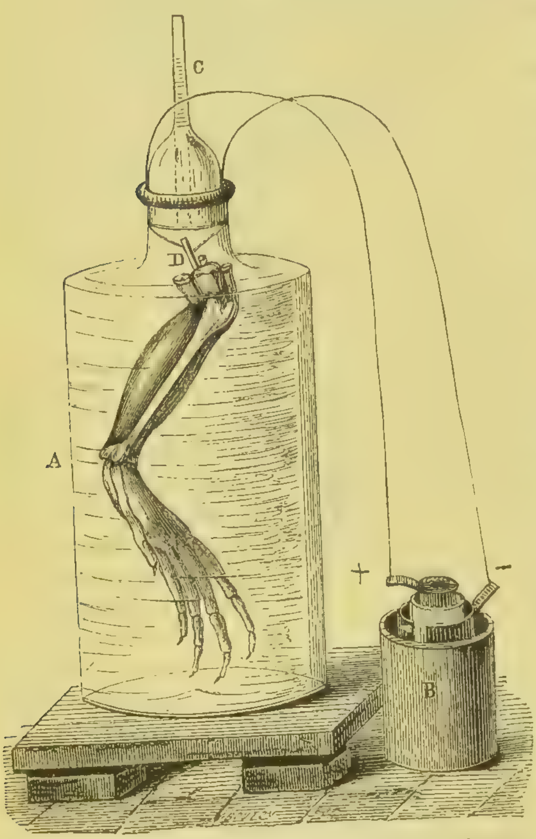


FIG. 159.—*Apparatus to show that muscles do not increase in volume during contraction.* (Marey.)
A, vessel of water, provided with a tube (C); B, galvanic apparatus; D, nerve, to which the stimulus is applied.

Notwithstanding the marked and constant changes in the form and consistence of the muscles during contraction, their actual volume is unchanged, or it undergoes modifications so slight that they may practically be disregarded. Experiments upon this point have been so uniform in their results, that it is hardly necessary to refer to them in detail. All modern observers accept the results of the older experiments, in which muscles have been made to contract in a vessel of water connected with a small upright tube, showing that, when the muscles are in active contraction as the result of a galvanic stimulus, the elevation of the liquid in the tube is unchanged. It is evident, therefore, that a muscle, while it hardens and changes in form during contraction, does not sensibly change in its actual volume.

Changes in the Form of the Muscular Fibres during Contraction.—It has been found exceedingly difficult to determine a question apparently so simple as that of the change in form which the muscular fibres undergo during contraction; and it is only of late years that this single point has been definitively settled. The idea that the fibres do not shorten, but that they assume a zigzag arrangement during contraction, is not adopted by any modern writers. All are now agreed that in muscular contraction there is an increase in the thickness of the fibre, exactly compensating its diminution in length. This has been repeatedly observed in microscopical examinations, and the only points now to determine are the exact mechanism of this transverse enlargement, its duration, the means by which it may be excited, and its physiological modifications. These questions, within the last few years, have been made the subjects of elaborate investigations by Helmholtz, Du Bois-Reymond, Aeby, Marey, and others; and, although it is hardly necessary to follow these experimenters through all of their investigations, many points have been developed, particularly by the system of registering the muscular movements, that possess considerable physiological importance.

One essential condition in the study of the mechanism of muscular contraction is to imitate, in a muscle or a part of a muscle that can be subjected to direct observation, the force that naturally excites it to contraction. The application of electricity to the nerve is beyond all question the most perfect method that can be employed for this purpose. We can in this way excite a single contraction, or, by employing a rapid succession of currents, we can excite either continuous or tetanic action. While the electric current is not identical with the nervous force, it is the best substitute we can employ in experiments upon muscular contractility, and it has the advantage of not affecting the physical and chemical integrity of the nervous and muscular tissue. In studying this subject, we shall first follow some of the experiments upon muscular contraction excited artificially, and then apply them, as far as possible, to the strictly physiological actions of muscles.

There are two classes of phenomena that may be produced by electrical excitation of motor nerves: 1. When the stimulus is applied in the form of a single discharge, it is followed by a single muscular contraction. 2. Under a rapid succession of discharges, the muscle is thrown into a state of permanent, or tetanic contraction. It will greatly facilitate our comprehension of the subject to study these phenomena separately and successively.

The muscular contraction produced by a single stimulus applied to the nerve is called by the French, *secousse* (shock), and by the Germans, *Zückung* (convulsion). It will be convenient for us to employ some term that will express this sudden action of the muscular fibres, as distinguished from the contraction that takes place on repeated stimulation or in continued muscular effort; and we shall designate a single muscular contraction, then, as spasm, applying the term tetanus, to continued action.

Spasm produced by Artificial Excitation.—If an electric discharge, even very feeble, be applied to a motor nerve connected with a fresh muscle, it is followed by a sudden contraction, which is succeeded by a rapid relaxation. Under this stimulation, the muscle shortens by about three-tenths of its entire length. The form of the contraction, as registered by the apparatus of Helmholtz, Marey, and others who have applied the so-called graphic method to the study of muscular action, presents certain interesting peculiarities. We shall give, however, only the general characters of this action, without discussing in detail the complicated apparatus employed.

According to Helmholtz, the whole period of a single contraction and relaxation of the gastrocnemius muscle of a frog is a little less then one-third of a second. The muscles of mammals and birds contract more rapidly, but, with this exception, the essential characters of the contraction are the same. The following are the periods occupied by these different phenomena:

Interval between stimulation and contraction	0″·020
Contraction	0″·180
Relaxation	0″·105
	0″·305

The duration of the electric current applied to the nerve is only 0″·0008. Contraction, however, does not follow immediately, there being an interval, called *pose*, of about one-fiftieth of a second. The contraction then follows, which is succeeded by gradual relaxation, the former being a little longer than the latter. This description represents the contraction of an entire muscle, but it does not indicate the changes in form of the individual fibres, a point much more difficult to determine satisfactorily. It is pretty well established, however, that a single fibre, with its irritability unimpaired, becomes contracted and swollen at the point where the stimulation is applied. Now, the question is whether, in normal contraction of the fibres in obedience to the natural nervous stimulus, there be a uniform shortening of the whole fibre, a shortening of those portions only that are the seat of the terminations of the motor nerves, or a peristaltic shortening and swelling, rapidly running the length of the fibre.

The recent experiments of Aeby, which have been repeated and extended by Marey, demonstrate beyond a doubt that, when one extremity of a muscle is excited, a contraction occurs at that point and is propagated along the muscle in the form of a wave, exactly like the peristaltic action of the intestines, except that it is more rapid. Both Aeby and Marey have succeeded in measuring the rapidity of the wave, and they find it to be about forty inches per second. Applying this principle to the physiological action of muscles, Aeby advances the theory that shortening of the fibres takes place wherever a stimulus is received, and that this is propagated in the form of a wave, which meets in its course another wave starting from a different point of stimulation. As we know that the motor nerves terminate at different points by becoming fused, as it were, with the sarcolemma, we can readily comprehend, under this theory, how the simultaneous contraction of all the fibres of a muscle is produced by stimulation of its motor nerve. This idea is expressed in the accompanying diagram. Although this view of the physiological action of the muscular fibres is extremely probable, it cannot be assumed that it has been absolutely demonstrated; but it is certainly more satisfactory and better sustained by experimental facts than any theory that has hitherto been advanced.

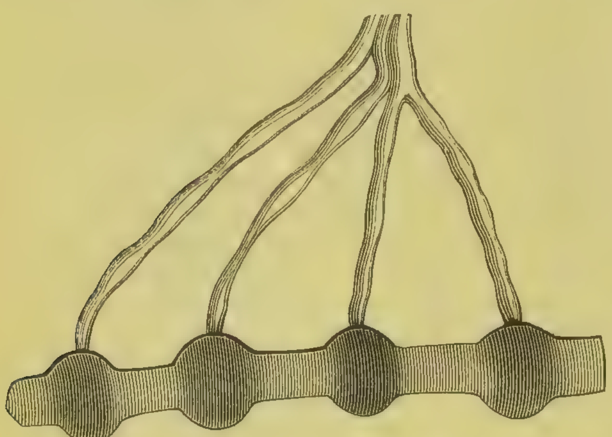


FIG. 160.—*Diagram of the muscular wave.* (Aeby.)

Mechanism of prolonged Muscular Contraction.—By a voluntary effort we are able to produce a muscular contraction of a certain duration, and of a power, within certain limits, proportionate to the amount of force we may desire to produce; but, after a certain time, the muscle becomes fatigued, and it may become exhausted to the extent that it will not respond to the normal stimulus. This is the kind of muscular action most interesting to us as physiologists.

The experiments of Marey seem to show precisely how far the nervous action that gives rise to a powerful and continuous muscular contraction can be imitated by electricity. Calling the movement produced by a single electric discharge, *secousse*, which we have translated by the word spasm, he calls the persistent contraction, tetanus. We shall adopt this name to distinguish persistent muscular action from the single contraction that we have just described.

It is a curious fact that a continued current of galvanic electricity passed through a nerve or a muscle does not induce muscular contraction; and it is only when the current is closed or broken, that any action is observed. But if we employ statical electricity, a muscular spasm occurs at every discharge, proportionate, in some degree, to the power of the excitation. If the discharges be very frequently repeated, or if a galvanic current be applied, broken by an interrupting apparatus, the spasms follow each other in quick succession. In experimenting upon the muscles of the frog, with a registering apparatus, Marey has found that, with a gradual increase in the rapidity of the electric shocks, the individual muscular spasms become less and less distinct, and that finally the contraction is permanent. His diagrams show well-marked spasms under ten excitations per second, a more complete fusion of the different acts with twenty per second, and a complete fusion, or tetanus, with twenty-seven per second. When the contraction had become continuous, there was an elevation in the line, showing increased power, as the excitations became more and more frequent. This is precisely the kind of contraction that occurs in the physiological action of muscles. Although the nervous force is not by any means identical with electricity, either the interrupted galvanic current or a succession of statical discharges is capable of producing a muscular action very like that which is involved in voluntary movements. The observations of Marey, showing that the intensity of what he terms artificial tetanic contraction is in proportion to the rapidity with which the electric discharges succeed each other, are exceedingly interesting in their practical applications; and an important question at once arises regarding the nervous force that excites voluntary motion. Is this a series of discharges, as it were, producing a power of muscular contraction in exact proportion to their rapidity? In view of the experiments just cited, this theory is very probable; and it is certain that the effect of a rapid succession of electric discharges almost exactly simulates the normal action of muscles. That vibrations, more or less regular, actually occur in muscular contraction, has been settled beyond a doubt by the researches of Wollaston, Haughton, and more lately by Helmholtz, the latter having recognized a musical tone in contracting muscles, exactly corresponding with the number of impressions per second made upon the nerve. He farther devised an ingenious method of recognizing the tone, by filling the ears with wax and contracting the temporal and masseter muscles. Marey has found, in repeating this experiment, that the tone may be changed by modifying the intensity of the muscular action. With the jaws feebly contracted, a grave sound is produced, and this can be raised one-fifth, by contracting the muscles as forcibly as possible.

The nerves are not capable of conducting an artificial stimulus for an indefinite period, nor are the muscles able to contract for more than a limited time upon the reception of such an excitation. The electric current may be made to destroy for a time both the nervous and muscular irritability; and these properties become gradually extinguished, the parts becoming fatigued before they are completely exhausted. Precisely the same phenomena are observed in the physiological action of muscles. When a muscle is fatigued artificially, a tetanic condition is excited more and more easily, but the intensity of the contraction proportionally diminishes. Muscles contracting in obedience to an effort of the will pass through the same stages of action. It is probable that constant contraction is excited more and more easily as the muscles become fatigued, because the nervous force gradually diminishes in intensity. It is certain that the vigor of contraction at the same time progressively diminishes.

Electric Phenomena in the Muscles.—It was ascertained a number of years ago, by Matteucci, that all living muscles are the seat of electric currents, which are not very powerful, it is true, but still are sufficiently marked to be detected by ordinary galvanometers. It is difficult, in the present state of our knowledge, to appreciate the physiological significance of this fact, and we shall therefore merely allude to the chief electric phenomena that are ordinarily observed, without attempting to follow out the elaborate and curious experiments since made by Du Bois-Reymond and others. One of the most simple methods of demonstrating this current is to prepare the leg of a frog with the crural nerve attached, and to apply one portion of the nerve to the deep parts of an incised muscle and the other to the surface. As soon as the connection is made, a contraction of the leg takes place. The same fact may be demonstrated with an ordinary galvanometer; but the evidence obtained by the frog's leg, when the experiment is properly performed, is sufficiently conclusive.

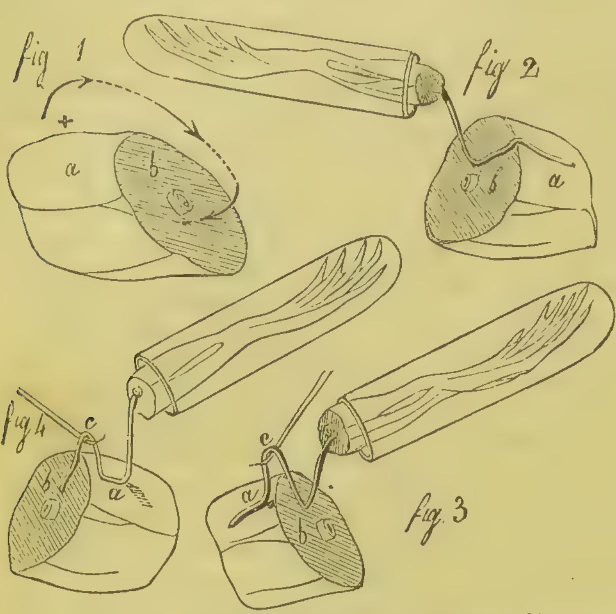


FIG. 161.—*Muscular current in the frog.* (Bernard.)
Fig. 1, portion of the thigh, with the skin removed; *a*, surface of the muscles; *b*, section; the direction of the current is indicated by the arrow.
Fig. 2, the nerve of a frog's leg (the leg enclosed in a glass tube) is applied to the section and the surface of the muscle. There is no contraction, because it is necessary that a portion of the nerve should be raised up.
Fig. 3, a portion of the nerve is raised with a glass rod. The contraction of the galvanoscopic leg occurs at the making of the circuit, because the current follows the course of the nerve, or is direct.
Fig. 4, the contraction here occurs at the breaking of the circuit, because the direction of the current is opposite the course of the nerve, or is inverse.

Matteucci constructed out of the fresh muscles from the thigh of the frog, what is sometimes called a frog-battery; which exhibits these currents in the most striking manner, their intensity being in direct ratio to the number of elements in the pile. To do this, he takes the muscles of the lower half of the thigh from several frogs, removing the bones, and arranges them in a series, each with its conical extremity inserted into the central cavity of the one below. In this way the external surface of each thigh except the last is in contact with the internal surface of the one below. If the two extremities of the pile be now connected with a galvanometer, quite a powerful current from the internal to the external surface of the muscle may be demonstrated. In a pile formed of ten elements, the needle of a galvanometer was deviated to from 30° to 40°.

Electric currents are observed in all living muscles, but they are most marked in the mammalia and warm-blooded animals. They exist, also, for a certain time after death. Artificial tetanus of the muscles, however, instead of intensifying the current, causes the galvanometer to recede. If, for example, the needle of the instrument show a deviation of 30° during repose, when the muscle is excited to tetanic contraction, it will return so as to mark only 10° or 15°. This phenomenon is observed only during a continued muscular contraction, and it does not attend a single spasm.

Muscular Effort.—The mere voluntary movement of parts of the body, when there is no obstacle to be overcome or no great amount of force is required, is very different from a muscular effort. For example, in ordinary progression there is simply a movement produced by the action of the proper muscles, almost without our consciousness, and this is unattended with any modification in the circulation or respiration; but, if we attempt to lift a heavy weight, to jump, to strike a powerful blow, or to make any vigorous effort, the action is very different. In the latter instance, we prepare for the muscular action by inflating the lungs, closing the glottis, and contracting more or less forcibly the expiratory muscles, so as to render the thorax rigid and unyielding; and, by a concentrated effort of the will, the proper muscles are then brought into action. This remarkable action of the muscles of the thorax and abdomen, due to simple effort and independent of the particular muscular act that is to be accomplished, compresses the contents of the rectum and bladder and obstructs very materially the venous circulation in the large vessels. It is well known that hernia is frequently produced in this way; the veins of the face and neck become turgid; the conjunctiva may become ecchymosed; and sometimes aneurismal sacs are ruptured. An effort of this kind is generally of short duration, and it cannot, indeed, be prolonged beyond the time during which respiration can be conveniently arrested. At its conclusion there is commonly a prolonged expiration, which is audible and somewhat violent at its commencement.

There are degrees of effort which are not attended with this powerful action of the muscles of the chest and abdomen, and in which the glottis is not completely closed; and an opening into the trachea or larynx, rendering immobility of the thorax impossible, does not interfere with certain acts that require considerable muscular power. If we examine a dog with the glottis exposed, when he makes violent efforts to escape, we can see that the opening is firmly closed. This fact we have often observed in vivisections; but Longet has shown that dogs with an opening into the trachea are frequently able to run and leap with "astonishing agility." He also saw a horse, with a large canula in the trachea, that performed severe labor and drew heavily-loaded wagons in the streets of Paris.

Passive Organs of Locomotion.

It would be out of place to describe fully and in detail all of the varied and complex movements produced by muscular action. Many of these, such as the movements of deglutition and of respiration, are necessarily considered in connection with the functions of which they form a part; but others are purely anatomical questions. Associated and antagonistic movements, automatic and reflex movements, etc., belong to the history of the motor nerves and will be fully considered under the head of the nervous system.

The study of locomotion involves a knowledge of the physiological anatomy of certain passive organs, the bones, cartilages, and ligaments. Although a complete history of the structure of these parts trenches somewhat upon the domain of anatomy, we are tempted to give a brief description of their histology, as it will complete our account of the tissues of the body, with the exception of the nervous system and the organs of generation, which will be taken up hereafter.

Locomotion is effected by the muscles acting upon certain passive, movable parts. These are the bones, cartilages, ligaments, aponeuroses, and tendons. We have already described the fibrous structures, and it only remains for us to study the bones and cartilages.

Physiological Anatomy of the Bones.—The number, classification, and relations of the bones are questions belonging to descriptive anatomy; and the only points we propose to consider refer to their general, or microscopical structure.

Every bone, be it long or short, is composed of what is called the fundamental substance, marked by microscopic cavities and canals of peculiar form. The cavities contain corpuscular bodies, called bone-corpuscles. The canals of larger size serve for the passage of blood-vessels, while the smaller canals (canaliculi) connect the cavities with each other and finally with the vascular tubes. Many of the bones present a medullary cavity, filled with a peculiar structure, called marrow. In almost all bones there are two distinct portions; one, which is exceedingly compact, and the other, more or less spongy or cancellated. The bones are also invested with a membrane, containing vessels and nerves, called the periosteum.

The method usually employed in the study of the bones is by thin sections made in various directions and examined either in their natural condition or with the calcareous matter removed by maceration in weak acid solutions. By the first method, we can make out the relations of the fundamental substance, the direction and relations of the vascular canals, and the form, size, relations, and connections of the bone-cavities and small canals. By the latter method, we can isolate and study the organic and corpuscular elements.

Fundamental Substance.—This constitutes the true bony substance, the medullary contents, vessels, nerves, etc., being simply accessory. It is composed of a peculiar organic matter, called osteine, combined with various inorganic salts, in which the phosphate of lime largely predominates. In addition to the phosphate of lime, the bones contain carbonate of lime, fluoride of calcium, phosphate of magnesia and of soda, and chloride of sodium. The relative proportions of the organic and inorganic matters are somewhat variable; but the average is about one-third of the former to two-thirds of salts. This proportion is necessary to the proper consistence and toughness of the bones.

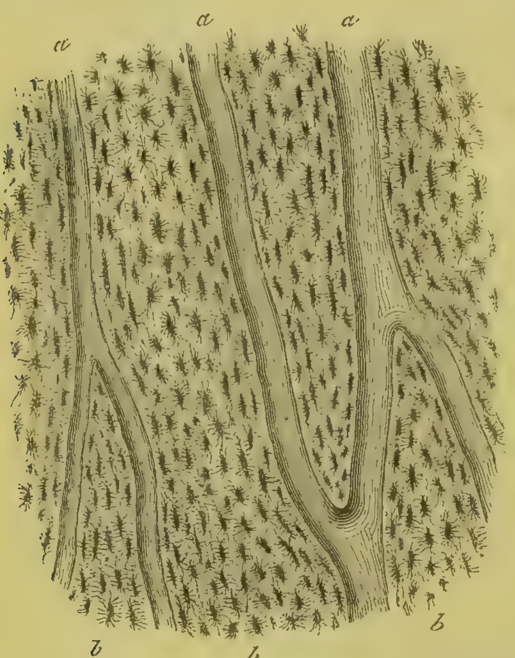


FIG. 162.—*Vascular canals and lacunæ, seen in a longitudinal section of the humerus; magnified 200 diameters.* (Sappey.)
a, a, a, vascular canals; b, b, b, lacunæ and canaliculi in the fundamental substance.

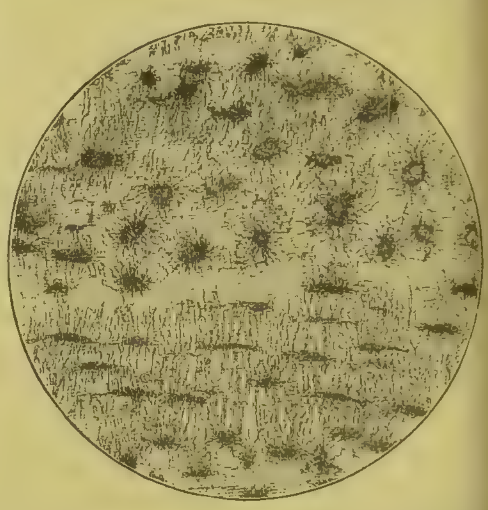


FIG. 163.—*Longitudinal section of bone, from the shaft of the human femur; magnified 150 diameters.* (From a photograph taken at the United States Army Medical Museum.)
This figure is introduced for the reason that it is a copy of a photograph of the actual structure.

Anatomically, the fundamental substance of the bones is arranged in the form of regular, concentric lamellæ, about $\frac{1}{3000}$ of an inch in thickness. This matter is of an indefinitely and faintly striated appearance, but it cannot be reduced to distinct fibres. In the long bones, the arrangement of the lamellæ is quite regular, surrounding the Haversian canals, and forming what are sometimes called the Haversian rods, following in their direction the length of the bone. In the short, thick bones the lamellæ are more irregular, frequently radiating from the central portion to the periphery. These peculiarities in the disposition of the fundamental substance will be more readily understood after a description of the Haversian canals.

The Haversian canals exist in the compact bony structure. They are either absent or very rare in the spongy and reticulated portions. Their form is rounded or ovoid, the larger canals being sometimes quite irregular. In the long bones their direction is generally longitudinal, although they anastomose by lateral branches. Each one of these canals contains a blood-vessel, and their disposition constitutes the vascular arrangement of the bones. They are all connected with the openings on the surface of the bones, by which the arteries penetrate and the veins emerge. Their size, of course, is variable. According to Sappey, the largest are about $\frac{1}{60}$ and the smallest, $\frac{1}{800}$ of an inch in diameter. Their average size is from $\frac{1}{250}$ to $\frac{1}{200}$ of an inch. In a transverse section of a long bone, the Haversian canals may be seen cut across and surrounded by from twelve to fifteen lamellæ. In a longitudinal section the course and anastomoses may be studied.

Lacunæ.—The fundamental substance is everywhere marked by irregular, microscopic excavations, of a peculiar form, called lacunæ or osteoplasts. These were at one time supposed to be corpuscles of calcareous matter and were known as the bone-corpuscles; but it has since been ascertained that this appearance is due to the imperfect methods of preparation of the thin sections of bone. They are connected with numerous little canals, giving them a stellate appearance. These are most numerous at the sides. The lacunæ measure from $\frac{1}{1250}$ to $\frac{1}{800}$ of an inch in their long diameter, by about $\frac{1}{2500}$ of an inch in width. They contain the true bone-corpuscles, which we shall presently describe.

Canaliculi.—These are little wavy canals, connecting the lacunæ with each other and presenting a communication between the first series of lacunæ and the Haversian

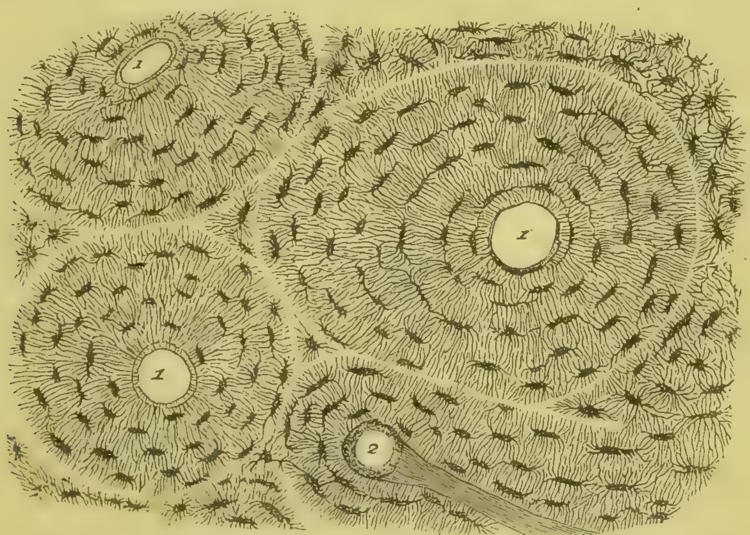


Fig. 164.—*Vascular canals and lacunæ, seen in a transverse section of the humerus; magnified* 200 *diameters.* (Sappey.)

1, 1, 1, section of the Haversian canals; 2, section of a longitudinal canal divided at the point of its anastomosis with a transverse canal. Around the canals, cut across perpendicularly, are seen the lacunæ (with their canaliculi), forming concentric rings.

canals. Each osteoplast presents from eighteen to twenty canaliculi radiating from its borders. Their length is from $\frac{1}{800}$ to $\frac{1}{600}$ of an inch, and their diameter, about $\frac{1}{25000}$ of an inch. The arrangement of the Haversian canals, lacunæ, and canaliculi is shown in Fig. 164.

Bone-cells or Corpuscles.—By treating perfectly fresh specimens of bone with weak acid solutions, Virchow has demonstrated the presence of stellate cells or corpuscles, exactly filling up the lacunæ and sending prolongations into the canaliculi. These structures have since been studied by Rouget, who has succeeded in demonstrating them in fresh bones from the fœtus, without using any reagent. They are stellate, granular, with a large nucleus and several nucleoli, and are of exactly the size and form of the lacunæ. They send out prolongations into the canaliculi, but it has been impossible to ascertain positively whether or not they form membranes lining the canaliculi throughout their entire length.

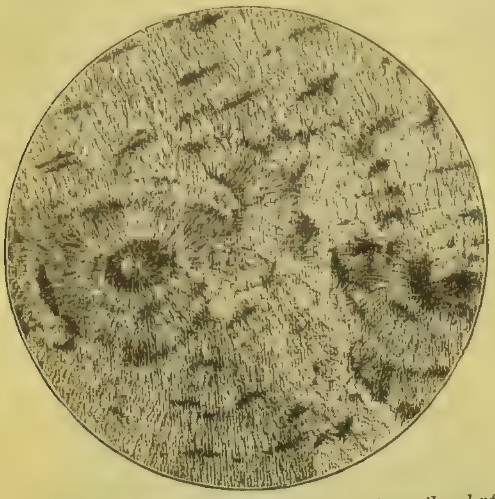


FIG. 165.—*Transverse section of bone, from the shaft of the human humerus; magnified 180 diameters.* (From a photograph taken at the United States Army Medical Museum.)
This figure is introduced for the reason that it is a copy of a photograph of the actual structure.

Marrow of the Bones.—The peculiar structure called marrow is found in the medullary cavities of the long bones, filling them completely and moulded to all the irregularities of their surface. It is also found filling the cells of the spongy portion. In other words, with the exception of the vascular canals, lacunæ, and canaliculi, the marrow fills all the spaces in the fundamental substance. We know very little of the functions of the marrow, and we shall therefore pass it over with a brief description.

It is now settled that the cavities of the bones are not lined with a membrane corresponding to the periosteum, and that the marrow is applied directly to the bony substance. In the fœtus and in very young children, the marrow is red and very vascular. In the adult it is yellow in some bones and gray or gelatiniform in others. It contains certain peculiar cells and nuclei, with amorphous matter, adipose vesicles, connective tissue, blood-vessels, and nerves.

Medullocells.—Robin has described little bodies, existing both in the form of cells and free nuclei, called medullocells. These are found in greater or less number in the

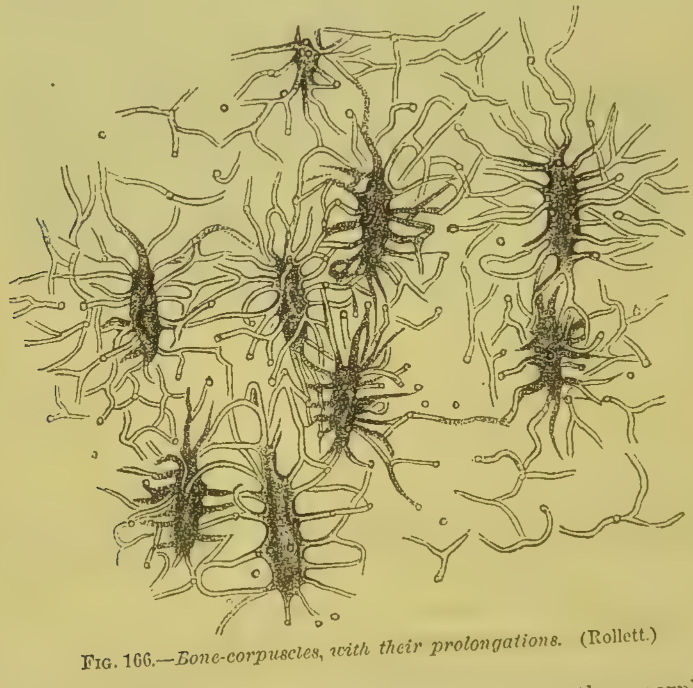


FIG. 166.—*Bone-corpuscles, with their prolongations.* (Rollett.)

bones at all ages, but they are more abundant in proportion as the amorphous matter and fat-cells are deficient. The nuclei are spherical, with borders sometimes irregular, generally without nucleoli, finely granular, and from $\frac{1}{5000}$ to $\frac{1}{3000}$ of an inch in diameter.

They are insoluble in acetic acid. The cells are less numerous than the free nuclei. They are spherical or slightly polyhedric, contain a few pale granulations, are rendered pale but are not dissolved by acetic acid, and they measure about $\frac{1}{1700}$ of an inch in diameter.

Myeloplaxes.—These are irregular, nucleated patches, also described by Robin, more abundant in the spongy portions of the bones than in the medullary canals, and are applied to the internal surfaces of the bones. They are exceedingly irregular in size and form (measuring from $\frac{1}{1250}$ to $\frac{1}{250}$ of an inch in diameter), are finely granular, and present from two to twenty or thirty nuclei. The nuclei are clear, ovoid, generally with a nucleolus, and are from $\frac{1}{3300}$ to $\frac{1}{2300}$ of an inch long, by $\frac{1}{5000}$ or $\frac{1}{4000}$ of an inch broad. The myeloplaxes are rendered pale by acetic acid, and the nuclei are then brought out more distinctly.

In addition to the anatomical elements just described, the marrow contains a few very delicate bundles of connective tissue, most of which accompany the blood-vessels. In the fœtus, the adipose vesicles are few or may be absent; but in the adult they are quite numerous, and in some bones they seem to constitute the whole mass of the marrow. They do not differ materially from the fat-cells in other situations. Holding these different structures together, is a variable quantity of semitransparent, amorphous, or slightly granular matter.

The nutrient artery of the bones sends branches to the marrow, generally two in number for the long bones, which are distributed between the various anatomical elements and finally surround the fatty lobules and the fat-vesicles with a delicate capillary plexus. The veins correspond to the arteries in their distribution. The nerves follow the arteries and are lost when these vessels no longer present a muscular coat. Nothing is known of the presence of lymphatics in any part of the bones or in the periosteum.

The only point of physiological interest connected with the marrow is, that it has been found to possess, in common with the periosteum but in a less degree, the property of generating true bony substances. We shall see farther on, that the periosteum is not only very important to the nutrition of the bones, but that it will generate bone when transplanted into vascular parts. M. Ollier, who has made a very extended series of experiments upon the physiological properties of the periosteum, endeavored to produce bone by transplanting portions of marrow, but was unsuccessful. M. Goujon, however, has lately been more fortunate. He has found that frequently, but not always, marrow transplanted into the muscular tissue will generate bone, particularly the marrow taken from young bones, but the bony tissue thus formed is soon absorbed.

Periosteum.—In most of the bones the periosteum presents a single layer of fibrous tissue, but in some of the long bones two or three layers may be demonstrated. This membrane adheres to the bone but can generally be separated without much difficulty. It covers the bones completely, except at the articular surfaces, where its place is supplied by cartilaginous incrustation. It is composed mainly of fibres of the white inelastic variety, with numerous small elastic fibres, blood-vessels, nerves, and a few adipose vesicles.

The arterial branches ramifying in the periosteum are quite numerous, forming a close, anastomosing plexus, which sends numerous small branches into the bony substance. There is nothing peculiar in the arrangement of the veins. The distribution of the veins in the bony substance has been very little studied.

The nerves of the periosteum are very abundant and form in its substance quite a close plexus.

The adipose tissue is very variable in quantity. In some parts it forms a continuous sheet, and in others the vesicles are scattered here and there in the substance of the membrane.

The importance of the periosteum to the nutrition of the bones is very great. Instances are on record where bones have been removed, leaving the periosteum, and in which the entire bone has been regenerated. The importance of the periosteum has been still farther illustrated by the remarkable experiments of M. Ollier, upon transplantation of this membrane in the different tissues of living animals.

Physiological Anatomy of Cartilage.—In this connection, the structure of the articular cartilages presents the chief physiological interest. The articular surfaces of all the bones are encrusted with a layer of cartilage, varying in thickness from $\frac{1}{50}$ to $\frac{1}{25}$ of an inch. The cartilaginous substance is white, opaline, and semitransparent when examined in thin sections. It is not covered with a membrane, but in the non-articular cartilages it has an investment analogous to the periosteum.

Examined in thin sections, cartilage is found to consist of a homogeneous fundamental substance, marked with numerous excavations, called cartilage-cavities, or chondroplasts. The intervening substance has a peculiar organic base, called cartilagine. By prolonged boiling this is changed into a new substance, called chondrine. The organic matter is united with a certain proportion of inorganic salts. This fundamental substance is elastic and resisting. The cartilages are closely united to the subjacent bony tissue. The free articular surface has already been described in connection with the synovial membranes.

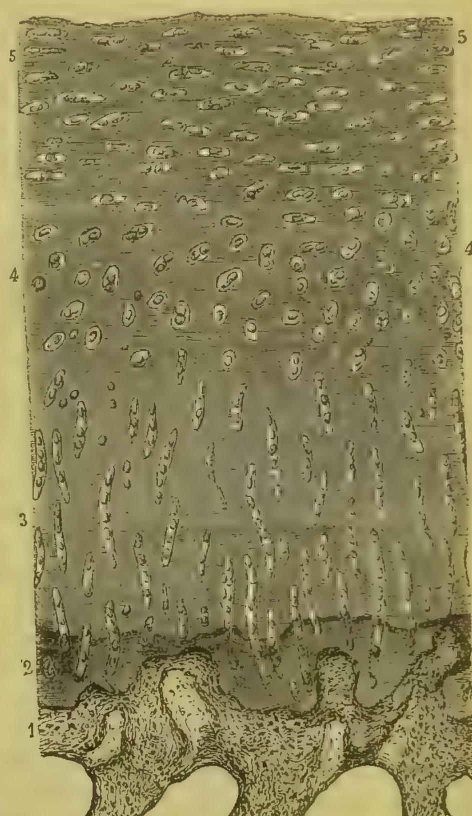


FIG. 168.—*Perpendicular section of a diarthrodial cartilage.* (Sappey.)

1, 1, osseous tissue; 2, 2, superficial layer of osseous tissue treated with hydrochloric acid; 3, 3, cavities and cells of the deep layer of cartilage; 4, 4, cavities and cells of the middle layer; 5, 5, cavities and cells of the superficial layer.

FIG. 167.—*Section of cartilage from the rib of the ox, showing the homogeneous fundamental substance, cartilage-cavities, and cartilage-cells; magnified 370 diameters.* (From a photograph taken at the United States Army Medical Museum.)

Cartilage-Cavities.—These cavities are rounded or ovoid, measuring from $\frac{1}{1250}$ to $\frac{1}{300}$ of an inch in diameter. They are generally smaller in the articular cartilages than in other situations, as in the costal cartilages. They are simple excavations in the fundamental substance, have no lining membrane, and contain a small quantity of a viscid liquid, with one or more cells. They are entirely analogous to the lacunæ of the bones.

Cartilage-Cells.—Near the surface of the articular cartilages, the cavities contain each a single cell; but in the deeper portions the cavities are long and contain from two to twenty cells arranged longitudinally. The cells are of about the size of the smallest cavities. They are ovoid, with a large, granular nucleus. They often contain a few small globules of oil. In the costal cartilages the cavities are not numerous but are rounded and quite large. The cells contain generally a certain amount of fatty matter. The appearance of the ordinary articular cartilage is represented in Fig. 168.

The ordinary cartilages have neither blood-vessels, lymphatics, nor nerves, and are nourished exclusively by imbibition from the surrounding parts. Their function has already been sufficiently considered in treating of the synovial membranes. In the development of the body, the anatomy of the cartilaginous tissue possesses peculiar interest, from the fact that the deposition of cartilage precedes the formation of bone; but we have here only to do with the permanent cartilages.

Fibro-Cartilage.—This variety of cartilage presents certain important peculiarities in the structure of its fundamental substance. It exists in the synchondroses, the cartilages of the ear, of the Eustachian tubes, the interarticular disks, the intervertebral cartilages, the cartilages of Santorini and of Wrisberg, and the epiglottis. Its structure has been very closely and successfully studied by Sappey, who has arrived at results differing considerably from those obtained by other observers.

According to Sappey, fibro-cartilage is composed of true fibrous tissue, with a great predominance of elastic fibres, fusiform, nucleated fibres, a certain number of adipose

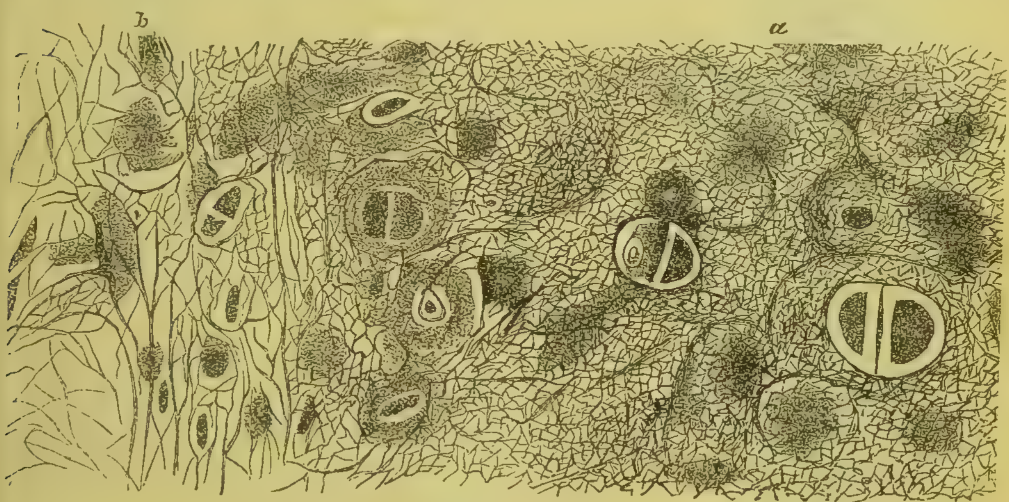


FIG. 169.—*Section of the cartilage of the ear of the human subject.* (Rollett.)
a, fibro-cartilage; *b*, connective tissue. In this preparation, the cartilage had been boiled and dried.

vesicles, cartilage-cells, and numerous blood-vessels and nerves. The presence of cartilage-cells assimilates this tissue to the ordinary cartilage, although its structure is very much more complex. The fibrous elements above mentioned take the place of the homogeneous fundamental substance of the true cartilage. The most important peculiarity in the structure of this tissue is that it is abundantly supplied with blood-vessels and nerves.

The reader is referred to works upon anatomy for a history of the action of the muscles. In some works upon physiology, will be found descriptions of the acts of walking, running, leaping, swimming, etc.; but we have thought it better to omit these subjects, rather than to enter as minutely as would be necessary into anatomical details and to give elaborate descriptions of movements which are simple and familiar.

Voice and Speech.

There are few subjects connected with human physiology of greater interest than the mechanism of voice and speech. In common with most of the higher classes of animals, man is endowed with voice; but, in addition, he is able to express by speech the ideas that are the result of the working of the brain. In this regard there is a difference between man and all other animals. It is the remarkable development and the peculiar properties of the brain that enable him to acquire the series of movements that constitute articulate language; and this faculty is nearly always impaired *pari passu* with deficiency in the intellectual endowment. Language is one of the chief expressions of intelligence; and its study, in itself, constitutes almost a distinct science, inseparably connected with psychology. In connection with the study of movements, therefore, it is not necessary to discuss the origin and construction of language, but simply to indicate the mechanism, first, of the formation of the voice, and afterward, the manner in which the voice is modified in the production of articulate sounds.

The voice in the human subject, presenting, as it does, a variety of characters as regards intensity, pitch, and quality, and being susceptible of great modifications by habit and cultivation, affords a very extended field for physiological study. Of late years, this has been the subject of careful investigation by the most eminent physicists and physiologists of the day; but to follow it out to its extreme limits requires a knowledge of the physics of sound and the theory of music, a full consideration of which would be inconsistent with the scope and objects of this work. We shall content ourselves, therefore, with a sketch of the physiological anatomy of the parts concerned in the formation of the voice, and the mechanism by which sounds are produced in the larynx, without treating fully of their varied modifications in quality. It will not be necessary to treat of the different theories of the voice that have been presented from time to time, except in so far as they have been confirmed by recent and complete observations, particularly those in which the vocal organs have been studied in action by means of the laryngoscope.

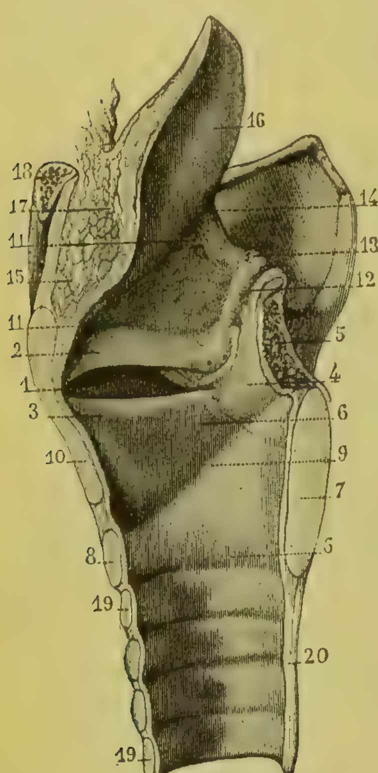


FIG. 170.—*Longitudinal section of the human larynx, showing the vocal chords.* (Sappey.)

1, ventricle of the larynx; 2, superior vocal chord; 3, inferior vocal chord; 4, arytenoid cartilage; 5, section of the arytenoid muscle; 6, 6, inferior portion of the cavity of the larynx; 7, section of the posterior portion of the cricoid cartilage; 8, section of the anterior portion of the cricoid cartilage; 9, superior border of the cricoid cartilage; 10, section of the thyroid cartilage; 11, 11, superior portion of the cavity of the larynx; 12, 13, arytenoid gland; 14, 16, epiglottis; 15, 17, adipose tissue; 18, section of the hyoid bone; 19, 19, 20, trachea.

Sketch of the Physiological Anatomy of the Vocal Organs.—The principal organ concerned in the production of the voice is the larynx. The accessory organs are the lungs, trachea, and expiratory muscles, and the mouth and resonant cavities about the face. The lungs furnish the air by which the vocal chords are thrown into vibration, and the mechanism of this action is merely a modification of the process of expiration. By the action of the expiratory muscles the intensity of vocal sounds is regulated. The trachea not only conducts the air to the larynx, but, by certain variations in its length and caliber, it may assist in modifying the pitch of the voice. Most of the variations in the tone and quality, however, are effected by the action of the larynx itself and of the parts situated above it.

It is impossible to give a complete account of the structure of the larynx, without going more fully than is desirable into purely anatomical details. Some anatomical points have already been referred to under the head of respiration, in connection with the respiratory movements of the glottis; and we propose here only to refer to the situation of the vocal chords, and to indicate the modifications that they can be made to undergo in their relations and tension by the action of certain muscles.

The vocal chords are stretched across the superior opening of the larynx from before backward. They consist of two pairs. The superior, called the false vocal chords, are not concerned in the production of the voice. They are less prominent than the inferior chords, although they have nearly the same direction. They are covered by an excessively thin mucous membrane, which is closely adherent to the subjacent tissue. The chords themselves are composed of fibres of the white inelastic variety, mixed with a few elastic fibres.

The true vocal chords are situated just below the superior chords. Their anterior attachments are near together, at the middle of the thyroid cartilage, and are immovable. Posteriorly they are attached to the movable arytenoid cartilages; and, by the action of certain muscles, their tension may be modified, and the chink of the glottis may be opened or closed. These ligaments are much larger than the false vocal chords, and they contain a very great number of elastic fibres. Like the superior ligaments, they are covered with an excessively thin and closely adherent mucous membrane. The mucous membrane over the borders of the chords is covered with pavement-epithelium without cilia. There are no mucous glands in the membrane covering either the superior or the inferior chords.

It has been conclusively shown that the inferior vocal chords alone are concerned in the production of the voice. Longet, who has made numerous experiments upon phonation, has demonstrated, by operations upon dogs, that the epiglottis, the superior vocal chords, and the ventricles of the larynx, may be injured, without producing any serious alteration in the voice, but that phonation becomes impossible after serious lesion of the inferior chords. This being the fact, as far as the mere production of the voice in the larynx is concerned, we have only to study the mechanism of the action of the inferior ligaments and the muscles by which their tension and relations are modified.

Muscles of the Larynx.—Anatomists usually divide the muscles of the larynx into extrinsic and intrinsic. The extrinsic muscles are attached to the outer surface of the larynx and to adjacent organs, such as the hyoid bone and the sternum. They are concerned chiefly in the movements of elevation and depression of the larynx. The intrinsic muscles are attached to the different parts of the larynx itself, and, by their action upon the articulating cartilages, are capable of modifying the condition of the vocal chords. The number of the intrinsic muscles is nine, consisting of four pairs and a single muscle. In studying the situation and attachments of these muscles, it will be useful at the same time to note their mode of action.

Bearing in mind the relations and attachments of the vocal chords, we can understand precisely how they can be rendered tense or loose by muscular action. Their fixed point is in front, where their extremities, attached to the thyroid cartilage, are nearly or quite in contact with each other. The arytenoid cartilages, to which they are attached posteriorly, present a movable articulation with the cricoid cartilage; and the cricoid, which is narrow in front, and is wide behind, where the arytenoid cartilages are attached, presents a movable articulation with the thyroid cartilage. It is evident, therefore, that muscles acting upon the cricoid cartilage can cause it to swing upon its two points of articulation with the inferior cornua of the thyroid, raising the anterior portion and approximating it to the lower edge of the thyroid; and, as a consequence, the posterior portion, which carries the arytenoid cartilages and the posterior attachments of the vocal chords, is depressed. This action would, of course, increase the distance between the arytenoid cartilages and the anterior portion of the thyroid, elongate the vocal chords, and subject them to a certain degree of tension. Experiments have shown that such an effect is produced by the contraction of the crico-thyroid muscles.

The articulations of the different parts of the larynx are such that the arytenoid cartilages may be approximated to each other posteriorly, though perhaps only to a slight extent, thus diminishing the interval between the posterior attachments of the vocal chords. This action can be effected by contraction of the single muscle of the larynx (the arytenoid) and also by the lateral crico-arytenoid muscles. The thyro-arytenoid muscles, the most complicated of all the intrinsic muscles in their attachments and the direction of their fibres, give rigidity and increased capacity of vibration to the vocal chords.

The posterior crico-arytenoid muscles, arising from each lateral half of the posterior surface of the cricoid cartilage and passing upward and outward to be inserted into the outer angle of the inferior portion of the arytenoid cartilages, rotate these cartilages outward, separate them, and act as dilators of the chink of the glottis. These muscles are chiefly concerned in the respiratory movements during inspiration.

The muscles mainly concerned in the modifications of the voice, by their action upon

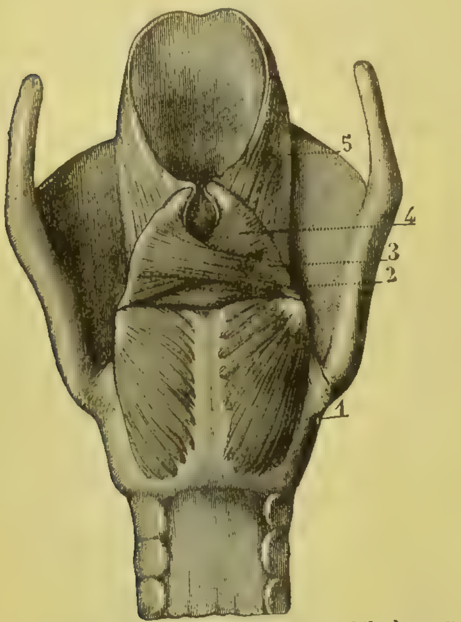


Fig. 171.—*Posterior view of the muscles of the larynx.* (Sappey.)

1, posterior crico-arytenoid muscle; 2, 3, 4, different fasciculi of the arytenoid muscle; 5, aryteno-epiglottidean muscle.

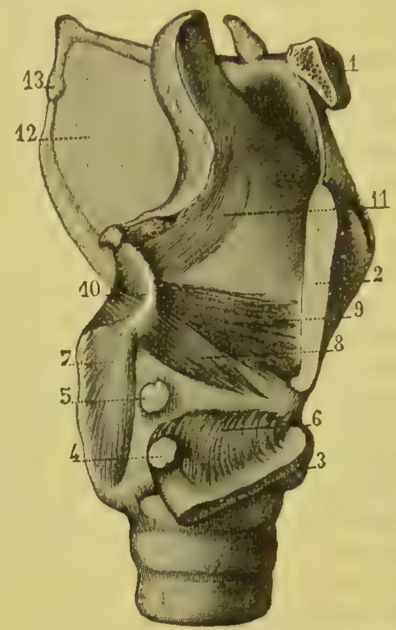


Fig. 172.—*Lateral view of the muscles of the larynx.* (Sappey.)

1, body of the hyoid bone; 2, vertical section of the thyroid cartilage; 3, horizontal section of the thyroid cartilage turned downward to show the deep attachment of the crico-thyroid muscle; 4, facet of articulation of the small cornu of the thyroid cartilage with the cricoid cartilage; 5, facet on the cricoid cartilage; 6, superior attachment of the crico-thyroid muscle; 7, posterior crico-arytenoid muscle; 8, 10, arytenoid muscle; 9, thyro-arytenoid muscle; 11, aryteno-epiglottidean muscle; 12, middle thyro-hyoid ligament; 13, lateral thyro-hyoid ligament.

the vocal chords, are the crico-thyroids, the arytenoid, the lateral crico-arytenoids, and the thyro-arytenoids. The following is a sketch of their attachments and mode of action:

Crico-thyroid Muscles.—These muscles are situated on the outside of the larynx at the anterior and lateral portions of the cricoid cartilage. Each muscle is of a triangular form, the base of the triangle looking posteriorly. It arises from the anterior and lateral portions of the cricoid cartilage, and its fibres diverge to be inserted into the inferior border of the thyroid cartilage, extending from the middle of this border posteriorly, as far back as the inferior cornua. Longet, after dividing the nervous filaments distributed to these muscles, noted hoarseness of the voice due to relaxation of the vocal chords; and, by imitating their action mechanically, he approximated the cricoid and thyroid cartilages in front, carried back the arytenoid cartilages, and rendered the chords tense.

Arytenoid Muscle.—This single muscle fills up the space between the two arytenoid cartilages and is attached to their posterior surface and borders. Its action evidently is to approximate the posterior extremities of the chords and to constrict the glottis, as far as the articulations of the arytenoid cartilages with the cricoid will permit. In any event, this muscle is important in phonation, as it serves to fix the posterior attachments of the vocal chords and to increase the efficiency of certain of the other intrinsic muscles.

Lateral Crico-arytenoid Muscles.—These muscles are situated in the interior of the larynx. They arise from the sides and superior borders of the cricoid cartilage, pass upward and backward, and are attached to the base of the arytenoid cartilages. By dividing all of the filaments of the recurrent laryngeal nerves, except those distributed to these muscles, and then galvanizing the nerves, Longet has shown that they act to approximate the vocal chords, and to constrict the glottis, particularly in its interligamentous portion. These muscles, with the arytenoid, act as constrictors of the larynx.

Thyro-arytenoid Muscles.—It is sufficiently easy to indicate the relations and attachments of these muscles, but their mode of action is more complex and difficult of comprehension. When we come to study the conditions of the vocal chords involved in certain modifications of the voice, we shall refer more in detail to the action of different fasciculi of these muscles. In this connection, we shall only describe very briefly their situation and attachments and the general results of their contraction.

The thyro-arytenoid muscles are situated within the larynx. They are broad and flat, and they arise in front from the upper part of the crico-thyroid membrane and the lower half of the thyroid cartilage. From this line of origin, each muscle passes backward in two fasciculi, both of which are attached to the anterior surface and the outer borders of the arytenoid cartilages. The application of galvanism to the nervous filaments distributed to these muscles has the effect of rendering the vocal chords rigid, increasing the intensity of their vibrations. The great variations that may be produced in the pitch and quality of the voice by the action of muscles operating directly or indirectly upon the vocal chords render the problem of determining the precise mode of action of the intrinsic muscles of the larynx exceedingly complicated and difficult. It is certain, however, that, in these muscular acts, the thyro-arytenoids play an important part. Their contraction regulates the thickness and rigidity of the vocal chords, while at the same time it modifies their tension. The swelling of the chords, which may be rendered regular and progressive under the influence of the will, is one of the most important agents in the formation of the timbre of the voice.

Mechanism of the Production of the Voice.

It will save much unprofitable discussion to dismiss quite briefly most of the theories that have been advanced to explain the production of the voice, and to avoid comparisons of the larynx with different kinds of musical instruments. Before the larynx had been studied in action by means of the laryngoscope, physiologists, having the anatomical structure of the parts for their only guide, presented various speculations with regard to the mechanism of phonation, which were frequently entirely opposed to each other in principle. The vocal apparatus was compared to wind or brass instruments, to reed-instruments, to string-instruments, to the flute, etc., and some even refused to the vocal chords any share in the sonorous vibrations. An apparatus was devised to imitate the vocal organs, experiments were made with the larynx removed from the body, and everything seemed to be done, indeed, except to observe the organs in actual function. A short time, however, after the laryngoscope came into use, the larynx was examined during the production of vocal sounds. The true value of previous theories was then positively demonstrated; and, while it has not been possible to settle all disputed points with regard to the precise mode of action of certain muscles, the appearances of the larynx itself during phonation and the results of the action of certain of the intrinsic muscles have been quite accurately described.

Appearance of the Glottis during Ordinary Respiration.—If the glottis be examined with the laryngoscope during ordinary respiration, the wide opening of the chink during inspiration, due to the action of the crico-arytenoid muscles, can be observed without difficulty. This action is effected by a separation of the posterior points of attachment of the vocal chords to the arytenoid cartilages. During ordinary expiration, none of the intrinsic muscles seem to act, and the larynx is entirely passive, while the air is gently forced out by the elasticity of the lungs and of the thoracic walls. But, as soon as an effort is made to produce a vocal sound, the appearance of the glottis undergoes a remarkable change, and it becomes modified in the most varied and interesting manner with the different changes in pitch and intensity that the voice can be made to assume. Although it is sufficiently evident that a sound may be produced, and even that words may be articulated, with the act of inspiration, true and normal phonation is effected during expiration only. It is evident, also, that the inferior vocal chords alone are concerned in this act. The changes in the position and tension of the chords we shall study, first with reference to the general act of phonation, and afterward, as the chords act in the varied modifications of the voice as regards intensity, pitch, and quality.

Movements of the Glottis during Phonation.—It is somewhat difficult to observe with the laryngoscope all of the vocal phenomena, on account of the epiglottis, which hides a considerable portion of the vocal chords anteriorly, especially during the production of certain tones; but the patience and skill of Garcia enabled him to overcome most of these difficulties, and to settle, by autolaryngoscopy, the most important questions with regard to the movements of the larynx in singing. It is fortunate that these observations, which are models of scientific accuracy and the result of most persevering study, were made by one profoundly versed, theoretically and practically, in the knowledge of music, and possessed of great control over the vocal organs.[1]

Garcia, after having observed the respiratory movements of the larynx, as we have briefly described them, noted that, as soon as any vocal effort was made, the arytenoid cartilages were approximated, so that the glottis appeared as a narrow slit formed by two chords of equal length, firmly attached posteriorly as well as anteriorly. The glottis thus undergoes a marked change. A nearly passive organ, opening widely for the passage of air into the lungs (because the inspiratory act has a tendency to draw its edges together) and entirely passive in expiration, has now become a sort of musical instrument, presenting a slit with borders capable of accurate vibration.

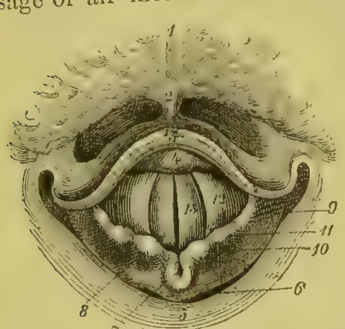


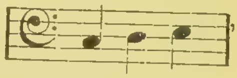
FIG. 173.—*Glottis seen with the laryngoscope during the emission of high-pitched sounds.* (Le Bon.)
1, 2, base of the tongue; 3, 4, epiglottis; 5, 6, pharynx; 7, arytenoid cartilages; 8, opening between the true vocal chords; 9, aryteno-epiglottidean folds; 10, cartilage of Santorini; 11, cuneiform cartilage; 12, superior vocal chords; 13, inferior vocal chords.

The approximation of the posterior extremities of the vocal chords and their tension by the action of certain of the intrinsic muscles are accomplished just before the vocal effort is actually made. The glottis being thus prepared for the emission of a particular sound, the expiratory muscles force air through the larynx with the required power. It seems wonderful how a carefully-trained voice can be modulated and varied in all its qualities, including the intensity of vibration, which is so completely under control; but, when we consider the changes in its quality, we must remember, in explanation, the varying conditions of tension and length of the vocal chords, the differences in the size of the larynx, trachea, and vocal passages generally, and the different relations that the accessory vocal organs can be made to assume. The power of the voice is simply due to the force of the expiratory act, which is regulated chiefly by the antagonistic rela-

[1] Manuel Garcia, the author of these observations, is the son of Garcia, the great composer and singer, and the brother of Mme. Malibran. He now enjoys a great reputation in London, as a singing-master; and his experiments were made with a view, if possible, of reducing the art of singing, which had always been taught according to purely empirical methods, to scientific accuracy. It is evident that this could be accomplished only through an exact knowledge of the mechanism of the production of vocal sounds.

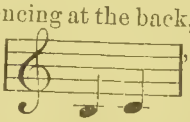
tions of the diaphragm and the abdominal muscles. From the fact that the diaphragm, as an active inspiratory muscle, is exactly opposed to the muscles which have a tendency to push the abdominal organs, with the diaphragm over them, into the thoracic cavity, and thus to diminish the pulmonary capacity, the expiratory and inspiratory acts may be balanced so nicely that the most delicate vocal vibrations can be produced. The glottis, thus closed as a preparation to a vocal act, presents a certain amount of resistance to the egress of air. This is overcome by the action of the expiratory muscles, and, with the passage of air through the chink, the edges of the opening, which are formed by the true vocal chords, are thrown into vibration. Many of the different qualities that are recognized in the human voice are due to differences in the length, breadth, and thickness of the vibrating ribbons; but, aside from what is technically known as quality, the pitch is dependent chiefly upon the length of the opening through which the air is made to pass and the degree of tension of the chords. The mechanism of these changes in the pitch of vocal sounds is well illustrated by Garcia in the following passage, which relates to what is known as the chest-voice:

"If we emit veiled and feeble sounds, the larynx opens at the notes

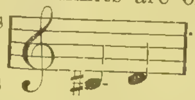

do, re, mi.

, and we see the glottis agitated by large and loose vibrations throughout its entire extent. Its lips comprehend in their length the anterior apophyses of the arytenoid cartilages and the vocal chords; but, I repeat it, there remains no triangular space.

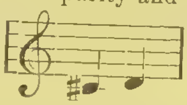
"As the sounds ascend, the apophyses, which are slightly rounded on their internal side, by a gradual apposition commencing at the back, encroach on the length of the glottis; and as soon as we reach the sounds


si, do.

, they finish by touching each other throughout their whole extent; but their summits are only solidly fixed one against the other at the notes


do, re.

. In some organs these summits are a little vacillating when they form the posterior end of the glottis, and two or three half-tones which are formed show a certain want of purity and strength, which is very well known to singers. From


do, re.

the vibrations, having become rounder and purer, are accomplished by the vocal ligaments alone, up to the end of the register.

"The glottis at this moment presents the aspect of a line swelled toward its middle, the length of which diminishes still more as the voice ascends. We shall also see that the cavity of the larynx has become very small, and that the superior ligaments have contracted the extent of the ellipse to less than one-half."

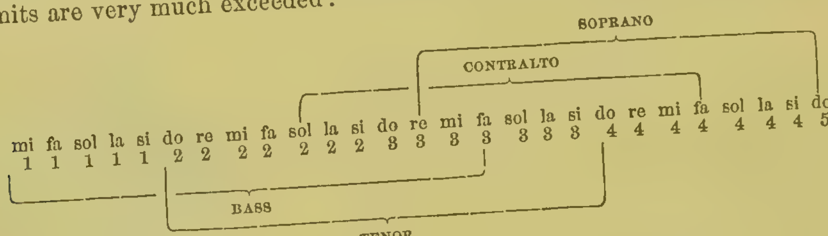
These observations have been in the main confirmed by Battaille, Emma Seiler, and all who have applied the laryngoscope to the study of the voice in singing. A few years ago we had an opportunity of observing the changes in the form of the glottis during the production of vocal sounds of different degrees of pitch, through the kindness of Dr. Ephraim Cutter, of Boston. In these experiments, the various points to which we have alluded were illustrated by autolaryngoscopy in the most marked manner; and nothing could be more striking than the changes in the form of the glottis in the transition from low to high notes. We have also frequently observed the general appearance of the glottis in phonation in experiments upon animals in which the glottis has been exposed to view.

Variations in the Quality of the Voice, depending upon Differences in the Size and Form of the Larynx and the Vocal Chords.—We are all sufficiently familiar with the characters of the male as distinguished from the female voice, and with what are known as the different vocal registers. In childhood, the general characters of the voice are essentially the same in both sexes. The larynx is smaller than in the adult, and the vocal muscles are evidently more feeble; but the quality of the vocal sounds at this period of life is peculiarly pure and penetrating. While there are certain characters that distinguish the voices of boys before the age of puberty, they present, as in the female, the different qualities of the soprano and contralto. At this age the voices of boys are capable of considerable cultivation, and their peculiar quality is sometimes highly prized in church-music. After the age of puberty, the female voice does not commonly undergo any very marked change, except in the development of additional strength and increased compass, the quality remaining the same; but in the male there is a rapid change at this time in the development of the larynx, and the voice assumes an entirely different quality of tone. This change does not usually take place if castration be performed in early life; and this operation was frequently resorted to in the seventeenth century, for the purpose of preserving the qualities of the soprano and contralto, particularly for church-music. It is only of late years, indeed, that this practice has fallen into disuse in Italy.

The ordinary range of all varieties of the human voice is given by Müller as equal to nearly four octaves; but it is rare that any single voice has a compass of more than two and a half octaves. There are examples, however, in which singers have acquired a compass of three octaves and even more. The celebrated singer, Mme. Parepa-Rosa, had a compass of voice that touches three full octaves, from sol$_2$ to sol$_5$. In music, the notes are written the same for the male as for the female voice, but the actual value of the female notes, as reckoned by the number of vibrations in a second, is always an octave higher than the male.

In both sexes there are differences, both in the range and the quality of the voice, which it is impossible for a cultivated musical ear to mistake. In the male, we have the bass and the tenor, with an intermediate voice, called the barytone. In the female, we have the contralto and the soprano, with the intermediate, or mezzo-soprano. In the bass and barytone, the lower and middle notes are the most natural and perfect; and, while the higher notes may be acquired by cultivation, they are not easy and do not possess the same quality as the corresponding notes of the tenor. The same remarks apply to the contralto and soprano. The mezzo-soprano is regarded by many as an artificial division.

The following scale, proposed by Müller, gives the ordinary ranges of the different kinds of voice; but it must be remembered that there are individual instances in which these limits are very much exceeded:



There is really no great difference in the mechanism of the different kinds of voice, and the differences in pitch are due chiefly to the greater length of the vocal chords in the low-pitched voices and to their shortness in the higher voices. The differences in quality are due to peculiarities in the conformation of the larynx, to differences in its size, and to variations in the size and form of the auxiliary resonant cavities. Great changes in the quality of the voice may be effected by practice. A cultivated note, for example, has an entirely different sound from a harsh, irregular vibration; and, by practice, a tenor may imitate the quality of the bass, and *vice versa*, although the effort is unnatural. It is not at all unusual to hear male singers imitate very closely the notes of the female, and the contralto will sometimes imitate the voice of the tenor in a surprisingly natural manner. These facts have a somewhat important bearing upon certain disputed points with regard to the mechanism of the different vocal registers, which will be considered farther on.

Action of the Intrinsic Muscles of the Larynx in Phonation.—It is much more difficult to find an entirely satisfactory explanation of the different tones produced by the human larynx in the action of the intrinsic muscles than to describe the changes in the tension and relations of the vocal chords. These muscles are concealed from view, and the only idea that we can have of their action is by reasoning from a knowledge of their points of attachment, and by operations upon the dead larynx, either imitating the contraction of special muscles or galvanizing the nerves in animals recently killed. In this way, as we have seen, some of the muscular acts have been studied very satisfactorily; but the precise effect of the contraction of certain of the muscles, particularly the thyro-arytenoids, is still a matter of discussion.

In the production of low chest-tones, in which the vocal chords are elongated and are at the mininum of tension that will allow of regular vibrations, the crico-thyroid muscles are undoubtedly brought into action, and these are assisted by the arytenoid and the lateral crico-arytenoids, which combine to fix the posterior attachments of the vibrating ligaments. It will be remembered that the crico-thyroids, by approximating the cricoid and thyroid cartilages in front, have a tendency to remove the arytenoid cartilages from the anterior attachment of the chords.

As the tones produced by the larynx become higher in pitch, the posterior attachments of the chords are approximated more firmly, and at this time the lateral crico-arytenoids are probably brought into vigorous action.

The function of the thyro-arytenoids is more complex; and it is probably in great part by the action of these muscles that the varied and delicate modifications in the rigidity of the vocal chords are produced.

The remarkable differences in singers as regards the purity of their tones are undoubtedly due in greatest part to the unswerving accuracy with which some put the vocal chords upon the stretch; while, in those in whom the tones are of inferior quality, the action of the muscles is more or less vacillating, and the tension is frequently incorrect. The fact that some celebrated singers can make the voice heard above the combined sounds from a large chorus and orchestra is not due entirely to the intensity of the sound, but in a great measure to the absolute mathematical equality of the sonorous vibrations and the comparative absence of discordant waves. Musicians who have heard the voice of the celebrated basso, Lablache, all bear testimony to the remarkable quality of his voice, which could be heard at times above a powerful chorus and orchestra. A grand illustration of this occurred at the musical festival at Boston, in 1869. In some of the solos by Mme. Parepa-Rosa, accompanied by a chorus of nearly twelve thousand, with an orchestra of more than a thousand and largely composed of brass instruments, we distinctly heard the pure and just notes of this remarkable soprano, standing alone, as it were, against the entire choral and instrumental force; and this in an immense building containing an audience of forty thousand persons. The absolute accuracy of the tone was undoubtedly an important element in its remarkably penetrating quality. In the same way we explain the fact that the flute, clarinet, or the sound from a Cremona violin, may be heard soaring above the chords of a full orchestra.

Action of Accessory Vocal Organs.—A correct use of the accessory organs of the voice is of the greatest importance in singing; but the manner in which these parts perform their function is exceedingly simple and does not require a very extended description. The human vocal organs, indeed, consist of a vibrating instrument, the larynx, and of certain tubes and cavities by which the sound is reënforced and modified.

The trachea serves, not only to conduct air to the larynx, but to reënforce the sound to a certain extent by the vibrations of the column of air in its interior. When a powerful vocal effort is made, it is easy to feel, with the finger upon the trachea, that the air contained in it is thrown into vibration. The structure of this tube is such that it may be elongated and shortened at will. In the production of low notes, the trachea is shortened and its caliber is increased, the reverse obtaining in the higher notes of the scale.

Coming to the larynx itself, we find that the capacity of its cavity is capable of certain variations. In fact, both the vertical and the bilateral diameters are diminished in high notes and are increased in low notes. The vertical diameter may be modified slightly by ascent and descent of the true vocal chords, and the lateral diameter may be reduced by the inferior constrictors of the pharynx, acting upon the sides of the thyroid cartilage.

The epiglottis, the superior vocal chords, and the ventricles, are by no means indispensable to the production of vocal sounds. In the formation of high notes, the epiglottis is somewhat depressed, and the superior chords are brought nearer together; but this only affects the character of the resonant cavity above the glottis. In low notes the superior chords are separated. It was before the use of the laryngoscope in the study of vocal phenomena that the epiglottis and the ventricles were thought to be so important in phonation. Undoubtedly the epiglottis has something to do with the character of the voice; but its function in this regard is not absolutely necessary, or even very important, as has been clearly shown in experiments of excising the part in living animals.

The most important modifications of the laryngeal sounds are produced by the resonance of air in the pharynx, mouth, and nasal fossæ. This resonance is indispensable to the production of the natural human voice. Under ordinary conditions, in the production of low notes the velum palati is fixed by the action of its muscular fibres, so that there is a reverberation of the bucco-pharyngeal and naso-pharyngeal cavities; that is, the velum is in such a position that neither the opening into the nose nor into the mouth is closed, and all of the cavities resound. As the notes are raised, the isthmus contracts, the part immediately above the glottis is also constricted, the resonant cavity of the pharynx and mouth is reduced in size, until finally, in the highest notes of the chest-register, the communication between the pharynx and the nasal fossæ is closed, and the sound is reënforced entirely by the pharynx and mouth. At the same time the tongue, a very important organ to singers, particularly in the production of high notes, is drawn back into the mouth. The point being curved downward, its base projects upward posteriorly and assists in diminishing the capacity of the cavity. In the changes which the pharynx thus undergoes in the production of different notes, the uvula acts with the velum and assists in the closure of the different openings. In singing up the scale, this is the mechanism, as far as the chest-notes extend. When, however, we pass into what is known as the head-voice, the velum palati is drawn forward instead of backward, and the resonance takes place chiefly in the naso-pharyngeal cavity.

Mechanism of the different Vocal Registers.—There has been a great deal of discussion, even among those who have studied the voice with the laryngoscope, with regard to the exact mechanism of the different vocal registers. It is now pretty well settled how the ordinary notes of what is known as the chest-register are produced; but, with regard to the falsetto, the difficulties in the way of direct observation are so great, that the question of its mechanism cannot be said to be definitively established.

The following are the vocal registers now recognized by most physiologists:

1. The chest-register, most powerful in male voices and in contraltos, and, indeed, almost characteristic of the male.

2. The falsetto register, which is the most natural voice of the soprano; though this voice is capable of chest-notes, not so full, however, as in the contralto or in the male. In the female this is known as the middle register.

3. The head-register, produced by a peculiar action of the glottis and the resonant cavities above the larynx. This is cultivated particularly in tenors and in the female.

Aside from the three registers, which belong to every voice, a practised ear can find no difficulty in distinguishing the different voices in nearly any part of the scale, both in the male and the female, by the following peculiarities: In the bass, the low notes are full, natural, and powerful, and the higher notes nearly always seem more or less artificial. In singing, the passage from the natural to the artificial notes in the scale is generally more or less apparent. In the tenor the full, natural notes are higher in the scale, the lower notes being almost always feeble and wanting in roundness. Corresponding peculiarities enable us to distinguish between the contralto and the soprano.

Chest-Register.—We shall simply recapitulate briefly the mechanism of the chest-notes, to enable us to study more easily the transitions to the different upper registers. This is the voice commonly used in speaking, and it is the most natural, the vocal ligaments vibrating according to their tension, as the air is forced through the larynx from the chest, and the air in the pharynx, mouth, and nasal fossæ producing a resonance without any artificial division of the different cavities. As the notes are elevated, the vocal chords are simply rendered more tense, and the parts above the larynx are more or less constricted, without any other change in the mechanism of the sound. But the chest-voice in the male cannot pass certain well-defined limits; and in the very highest notes it must be merged either into the head-voice or the falsetto. The falsetto, however, is now but little cultivated, although some tenor singers, after long practice, succeed in making the change from one register to the other so nicely that it is hardly perceptible, even to a cultivated ear. The head-voice has essentially the same mechanism in the male as in the female, and this will be considered after we have discussed the falsetto, which is the natural voice of soprano singers.

Falsetto Register.—The difference of opinion among laryngoscopists with regard to the mechanism of the falsetto is probably in great part due to the fact that, when these notes are produced, the isthmus of the fauces is so powerfully contracted that it becomes exceedingly difficult to study the action of the vocal chords. There is no reason for supposing that the mechanism of this register does not involve vibration of the true vocal chords, as in the chest-voice, the difference being in the tension and in the extent of the vibrating portion. According to the observations of Fournié, in the falsetto the tongue is pressed strongly backward and the epiglottis is forced over the larynx. Mrs. Emma Seiler, from an extended series of autolaryngoscopic observations, has arrived at the conclusion that this voice involves vibrations of the fine, thin edges of the chords only, a greater width vibrating in the production of the chest-voice. She is particularly careful to insist upon the distinction between the falsetto and the head-register, the latter being produced by an entirely different mechanism. On the whole, this explanation seems to be the most satisfactory.

It must be remembered that the distinction between the chest-register or the head-register and the falsetto, as far as pitch is concerned, is not absolute. Certain of the high notes of the chest or the head-voice, for example, may be produced in the falsetto. In the cultivation of the female voice, Mrs. Seiler considers that it is exceedingly important not to strain the chest-voice to its highest point, but to use each register in its normal place in the scale, taking care, by practice, to render the transition from one to the other natural and agreeable. We have heard male singers, probably endowed with peculiar vocal powers, who were able, by the use of the falsetto, to imitate almost exactly the soprano voice, though without the sweetness and purity of tone characteristic of the perfect female organ. In the same way, by straining the chest-voice beyond its normal limits, some females, particularly contraltos, are able to produce a very good imitation of the tenor quality.

Head-Register.—This voice is highly cultivated, particularly in tenors and in the best female singers. It is not to be confounded, however, with the falsetto, as was done by some physiologists before the invention of the laryngoscope. Head-notes may be produced by cultivated male singers, bass and barytone, as well as tenor; but the former seldom have occasion for any but the chest-notes. Still, there are musical passages in which the *sotto-voce* head-notes of the bass have an exquisite softness and are used with great effect. We have already stated that, in the transition to the head-voice, the velum palati is applied to the base of the tongue, and the sound is reënforced by resonance from the naso-pharyngeal cavity. If this be its mechanism, its study with the laryngoscope must be exceedingly difficult.

The most important theory of the mechanism of the head-voice has been proposed by Mrs. Seiler. After long and patient effort, she was able to expose the glottis during the production of these notes, when it was found that the vocal chords were firmly approximated posteriorly, leaving an oval opening, with vibrating edges, involving only one-half or one-third of the vocal ligaments. This orifice contracted progressively with the higher notes. This peculiar division of the vocal ligaments is due, according to Mrs. Seiler, to the action of a muscular bundle, called the internal thyro-arytenoid, upon little cartilages (the cuneiform) extending forward from the arytenoid cartilage, in the substance of the vocal ligaments, as far as the middle of the glottis.

With proper cultivation, the transition from the middle register to the head-voice in the female may be effected almost imperceptibly, thereby increasing the compass from three to six notes, and even more; and in the male the same may be accomplished without difficulty, particularly in tenors. There can be hardly any doubt of the fact that the naso-pharyngeal space is chiefly concerned in the resonance that takes place in head-notes, though its actual demonstration is very difficult. The distinction between the head and the chest notes is fully as marked in the male as in the female; but it must be remembered that one of the great ends to be accomplished in the cultivation of the human voice is to make the three registers pass into each other so that they shall appear as one.

Mechanism of Speech.

Articulate language consists in a conventional series of sounds made for the purpose of conveying certain ideas. There being no universal language, we must confine our description of the faculty of speech to the mode of production of the language in which this work is written. Language, as it is naturally acquired, is purely imitative and does not involve of necessity the construction of an alphabet, with its combinations into syllables, words, and sentences; but, as civilization has advanced, we have been taught to associate certain differences in the accuracy and elegance with which ideas are expressed, with the degree of development and cultivation of the intellectual faculties. Philologists have long since established a certain standard—varying, to some extent, it is true, with usage and the advance of knowledge, but still sufficiently definite—by which the correctness of modes of expression is measured. We do not propose to discuss the science of language, or to consider, in this connection, at least, the peculiar mental operations concerned in the expression of ideas, but to take our own tongue as we find it, and describe briefly the mechanism of the production of the most important articulate sounds.

Almost every language is imperfect, as far as an exact correspondence between its sounds and written characters is concerned. Our own language is full of incongruities in spelling, such as silent letters and arbitrary and unmeaning variations in pronunciation; but these do not belong to the subject of physiology. There are, however, certain natural divisions of the sounds as expressed by the letters of the alphabet.

Vowels.—Certain articulate sounds are called vowel, or vocal, from the fact that they are produced by the vocal chords and are but slightly modified as they pass out of the mouth. The true vowels, *a*, *e*, *i*, *o*, *u*, can all be sounded alone and may be prolonged in expiration. These are the sounds chiefly employed in singing. The differences in their characters are produced by changes in the position of the tongue, mouth, and lips. The vowel-sounds are necessary to the formation of a syllable, and, although they are generally modified in speech by consonants, each one may, of itself, form a syllable or a word. In the construction of syllables and words, the vowels have many different qualities, the chief differences being as they are made long or short. In addition to the modifications in the vowel-sounds by consonants, two or three may be combined so as to be pronounced by a single vocal effort, when they are called respectively, diphthongs and triphthongs. In the proper diphthongs, as *oi*, in voice, the two vowels are sounded. In the improper diphthongs, as *ea*, in heat, and in the Latin diphthongs, as *æ*, in Cæsar, one of the vowels is silent. In triphthongs, as *eau*, in beauty, only one vowel is sounded. *Y*, at the beginning of words, is usually pronounced as a consonant; but in other situations it is pronounced as *e* or *i*.

A very curious and interesting inquiry relates to the differences, with which we are all familiar, in the quality of the different vowel-sounds when pronounced with equal pitch and intensity. The cause of these differences was studied very closely in the latter part of the last century, but it has lately been rendered very clear by the elaborate and convincing researches of Helmholtz. In this connection, it will be sufficient to indicate the results of modern investigations very briefly. When we come to study the physics of sound in connection with the sense of hearing, we shall see that nearly all sounds, even when produced by a single vibrating body, are compound. Helmholtz, by means of his resonators, has succeeded in analyzing the apparently simple sounds into different component parts, and he has shown that the quality of such sounds may be modified by reënforcing certain of the overtones, as they are called, such as the third, fifth, or octave. For those who are familiar with the physics of sound, the explanation which we shall give of the mechanism of the production of vowel-sounds will be readily comprehensible. The reader is referred, however, to our remarks upon overtones in another part of this work, under the head of audition, for a more thorough exposition of this subject. This should be read in connection with what we shall say here of vowel-sounds, when the whole subject will be sufficiently clear. We may pronounce the different vowel-sounds with the same pitch and intensity, but the sound in each is different, on account of variations in the resonant cavities of the accessory vocal organs, especially the mouth. It has been ascertained experimentally that the overtones in each instance are different, as they are reënforced by the vibrations of air in the accessory vocal organs, in some instances the third, in others, the fifth, etc., being increased in intensity. We cannot illustrate this better than by the following quotation from Tyndall, in which modern researches have been applied to the vowel-sounds of our own language:

"For the production of the sound *U* (*o o* in hoop), I must push my lips forward so as to make the cavity of the mouth as deep as possible, at the same time making the orifice of the mouth small. This arrangement corresponds to the deepest resonance of which the mouth is capable. The fundamental tone of the vocal chords is here reënforced, while the higher tones are thrown into the shade. The *U* is rendered a little more perfect when a feeble third tone is added to the fundamental.

"The vowel *O* is pronounced when the mouth is so far opened that the fundamental tone is accompanied by its strong higher octave. A very feeble accompaniment of the third and fourth is advantageous, but not necessary.

"The vowel *A* derives its character from the third tone, to strengthen which by resonance the orifice of the mouth must be wider, and the volume of air within it smaller than in the last instance. The second tone ought to be added in moderate strength, whilst weak fourth and fifth tones may also be included with advantage.

"To produce *E* the fundamental tone must be weak, the second tone comparatively strong, the third very feeble, but the fourth, which is characteristic of this vowel, must be intense. A moderate fifth tone may be added. No essential change, however, occurs in the character of the sound when the third and fifth tones are omitted. In order to exalt the higher tones which characterize the vowel-sound *E*, the resonant cavity of the mouth must be small.

"In the production of the sound *ah!* the higher overtones come principally into play; the second tone may be entirely neglected; the third rendered feebly; the higher tones, particularly the fifth and seventh, being added strongly.

"These examples sufficiently illustrate the subject of vowel-sounds. We may blend in various ways the elementary tints of the solar spectrum, producing innumerable composite colors by their admixture. Out of violet and red we produce purple, and out of yellow and blue we produce white. Thus also may elementary sounds be blended so as to produce all possible varieties of clang-tint. After having resolved the human voice into its constituent tones, Helmholtz was able to imitate these tones by tuning-forks, and, by combining them appropriately together, to produce the clang-tints of all the vowels."

Consonants.—Some of the consonants have no sound in themselves and serve merely to modify vowel-sounds. These are called mutes. They are *b*, *d*, *k*, *p*, *t*, and *c* and *g* hard. Their office in the formation of syllables is sufficiently apparent.

The consonants known as semivowels are, *f*, *l*, *m*, *n*, *r*, *s*, and *c* and *g* soft. These have an imperfect sound of themselves, approaching in character the true vowel-sounds. Some of these, *l*, *m*, *n*, and *r*, from the facility with which they flow into other sounds, are called liquids. Orthoepists have farther divided the consonants with reference to the mechanism of their pronunciation: *d*, *j*, *s*, *t*, *z*, and *g* soft, being pronounced with the tongue against the teeth, are called dentals; *d*, *g*, *j*, *k*, *l*, *n*, and *q* are called palatals; *b*, *p*, *f*, *v*, and *m* are called labials; *m*, *n*, and *ng* are called nasals; and *k*, *q*, and *c* and *g* hard are called gutturals. After the description we have given of the voice, it is not necessary to discuss farther the mechanism of these simple acts of articulation.

For the easy and proper production of articulate sounds, absolute integrity of the mouth, teeth, lips, tongue, and palate is required. We are all acquainted with the modifications in articulation, in persons in whom the nasal cavities resound unnaturally, from imperfection of the palate; and the slight peculiarities observed after loss of the teeth and in hare-lip are sufficiently familiar. The tongue is generally regarded, also, as an important organ of speech, and this is the fact in the great majority of cases; but instances are on record in which distinct articulation has been preserved after complete destruction of this organ. These cases, however, are unusual, and they do not invalidate the great importance of the tongue in ordinary speech.

It is thus seen that speech consists essentially in a modification of the vocal sounds by the accessory organs, or by parts situated above the larynx; the latter being the true vocal instrument. While the peculiarities of pronunciation in different persons and the difficulty of acquiring foreign languages after the habits of speech have been formed show that the organs of articulation must perform their function with great accuracy, their movements are simple, and they vary with the peculiarities of different languages. The most interesting question, in its general physiological relations, is that to which a great part of this chapter has been devoted; and that is the mechanism of the production of the voice.

CHAPTER XVII.

PHYSIOLOGICAL DIVISIONS, STRUCTURE, AND GENERAL PROPERTIES OF THE NERVOUS SYSTEM.

General considerations—Divisions of the nervous system—Physiological anatomy of the nervous tissue—Anatomical divisions of the nervous tissue—Medullated nerve-fibres—Simple, or non-medullated nerve-fibres—Gelatinous nerve-fibres (fibres of Remak)—Accessory anatomical elements of the nerves—Branching and course of the nerves—Termination of the nerves in the muscular tissue—Termination of the nerves in glands—Terminations of the sensory nerves—Corpuscles of Pacini, or of Vater—Tactile corpuscles—Terminal bulbs—Structure of the nerve-centres—Nerve-cells—Connection of the cells with the fibres and with each other—Accessory anatomical elements of the nerve-centres—Composition of the nervous substance—Regeneration of the nervous tissue—Reunion of nerve-fibres—Motor and sensory nerves—Distinct seat of the motor and sensory properties of the spinal nerves—Experiments of Magendie upon the roots of the spinal nerves—Properties of the posterior roots of the spinal nerves—Properties of the anterior roots of the spinal nerves—Recurrent sensibility—Mode of action of the motor nerves—Associated movements—Mode of action of the sensory nerves—Sensation in amputated members—General properties of the nerves—Nervous irritability—Different means employed for exciting the nerves—Disappearance of the irritability of the motor and sensory nerves after exsection—Nerve-force—Rapidity of nervous conduction——Estimation of the duration of acts involving the nerve-centres—Action of electricity upon the nerves—Induced muscular contraction—Galvanic current from the exterior to the cut surface of a nerve—Effects of a constant galvanic current upon the nervous irritability—Electrotonus, anelectrotonus, and catelectrotonus—Neutral point—Negative variation.

The nervous system is anatomically distinct in all animals except those lowest in the scale of being. It is useless to speculate upon the question of the existence of matter endowed with properties analogous to those observed in the nervous system of the higher animals, in beings so low in their organization as to present no divisions into anatomical elements; for the present condition of physiological science does not admit of the recognition of functions without organs. All animals that present any thing like nervous functions present also an anatomically distinct nervous system. Within certain limits, the perfection of the animal organization depends upon the general development of the nervous system.

High in the animal scale, as in the warm-blooded animals, the general development of the nervous system presents little if any variation; but special attributes are coexistent with the development of special organs. The development in this way of particular portions of the nervous system is in accordance with the peculiar conditions of existence of different animals; it is a necessary part of their organization, and is not dependent upon education or intelligence. Examples of this are in the extraordinary development of the sense of sight, hearing, or smell, in different animals. There are animals in which these special senses possess a delicacy of perception to which man, even with the greatest amount of intelligent education, can never attain; but man, possessing a nervous organization not superior to that of other warm-blooded animals in its general development, and inferior to many in the development of special organs, stands immeasurably above all other beings, by virtue of the immense preponderance of what is known as the encephalic portion of the nervous system.

These brief general considerations will convey some idea of the physiological importance of the nervous system; of the care which should be exercised in its study; and of the great interest attached to it, from the fact that the most complex and important of its functions belong to human physiology, and to human physiology alone.

We can best define what is to be included under the head of the nervous system, by citing certain of its prominent and well-established properties and functions:

1. The nervous system is anatomically and physiologically distinct from all other systems and organs in the body. It receives impressions made upon the terminal branches of its sensory portion and it conveys stimulus to parts, determining and regulating the operation of their functions; but its physiological properties are inherent, and it gives to no

tissue or organ its special "irritability" or the power of performing its particular function.

2. The nervous system connects into a coördinated organism all parts and organs of the body. It is the medium through which all impressions are received. It animates or regulates all movements, voluntary and involuntary. It regulates the functions of secretion, nutrition, calorification, and all the processes of organic life.

In addition to its functions as a medium of conduction and communication, the nervous system, in certain of its parts, is capable of receiving impressions and of generating a stimulating influence, or force, peculiar to itself. As there can be no physiological connection or coördination of different parts of the organism, having an active function, without nerves, there can be no unconscious reception of impressions giving rise to involuntary movements, no appreciation of impressions, general, as in ordinary sensation, or special, as in sight, smell, taste, or hearing, no instinct, volition, thought, or even knowledge of existence, without nerve-centres.

Possessing, as it does, these varied properties and functions, it is evidently of the greatest physiological importance that the anatomical characters of the nervous system should be most carefully studied, with a view of connecting, if possible, certain of the nervous properties with peculiarities in structure. It is also important to subdivide the system, as regards general properties and functions, as well as with reference to the special office of particular parts. With this end in view, we shall point out first, the great anatomico-physiological divisions common to nervous matter wherever it exists, and afterward, the subdivisions of the system as regards special functions.

Divisions of the Nervous System.

Nervous matter, whatever may be its special function, presents two great divisions, each with distinct anatomical as well as physiological differences. One of these divisions presents the form of fibres or tubes. This kind of nervous matter is incapable of generating a force or stimulus, and it serves only as a conductor. The other division is in the form of cells, and this kind of nervous matter alone is capable of generating the so-called nervous force.

The nervous matter is divided into two great systems, as follows:

1. The cerebro-spinal system, composed of the brain and spinal cord with the nerves directly connected with these centres. This system is specially connected with the functions of relation, or of animal life. The centres preside over general sensation, the special senses, voluntary and some involuntary movements, intellection, and, in short, all of the functions that characterize the animal. The nerves serve as the conductors of impressions known as general or special sensations, and of the stimulus that gives rise to voluntary and certain involuntary movements, the latter being the automatic movements connected with animal life.

2. The sympathetic, or organic system. This system is specially connected with the functions relating to nutrition, operations which have their analogue in the vegetable kingdom and are sometimes called the functions of vegetative life. Although this system presides over functions entirely distinct from those characteristic of and peculiar to animals, the centres of this system all have an anatomical and physiological connection with the cerebro-spinal nerves.

The cerebro-spinal system is subdivided into centres presiding over movements and ordinary sensation, and centres capable of receiving impressions connected with the special senses, such as sight, audition, olfaction, and gustation. The nerves which receive these special impressions and convey them to the appropriate centres are more or less insensible to ordinary impressions. The organs to which these special nerves are distributed are generally of a complex and peculiar structure, and they present numerous accessory parts which are important and essential in the transmission of the special impressions to the terminal branches of the nerves.

In treating of the nervous system, we shall consider first the physiological anatomy of the nervous tissue; next, the general properties of the cerebro-spinal system; next, the functions of different portions of this system connected with motion, ordinary sensibility, intellection, etc.; next, the functions of the sympathetic, or organic system of nerves; and finally, the special senses, with the physiological anatomy and mechanism of the accessory parts.

Physiological Anatomy of the Nervous Tissue.

The physiological anatomy of the nervous system naturally divides itself into two sections; one embracing what is called the general anatomy of the nervous tissue, and the other, the arrangement of this tissue in special organs, as far as this is connected with their functions.

The intimate structure of the different portions of the nervous system may now be regarded as tolerably well understood, at least so far as those anatomical points bearing upon physiology are concerned. The connection between the nerve-cells and the fibres and the modes of termination of the motor filaments in the muscles are points nearly if not quite settled; and the terminations of sensory filaments in integument and mucous membranes have lately been investigated very thoroughly and with quite positive and satisfactory results. These anatomical points are specially connected with the general properties of the nervous system, both as a generator of the so-called nerve-force and as a conductor.

The arrangement of the nervous elements in special organs, as in the brain and spinal cord, has not been so successfully investigated and presents immense difficulties in its study; and we can hardly hope to acquire any thing like a definite and thorough knowledge of the functions of these parts, until we have much more positive information concerning their anatomical characters.

Anatomical Divisions of the Nervous Tissue.—The physiological division of the nervous system into nerves and nerve-centres is pretty well carried out as regards the anatomical structure of these parts. The two great divisions of the system, anatomically considered, are into nerve-cells and nerve-fibres.

The nerve-cells, as far as we know, are the only parts capable, under any circumstances, of generating the nerve-force; and, as a rule, they cannot receive impressions in any other way than through the nerve-fibres. There are, however, some exceptions, either apparent or real, to this rule, as in the case of direct irritation of the ganglion of the tuber annulare, portions of the cerebrum, and the sympathetic ganglia, which seem sensible to direct irritation; but the cells of most of the ganglia belonging to the great cerebro-spinal axis are insensible to direct stimulation and can only receive impressions conducted to them by the nerves.

The nerve-fibres act only as conductors and are incapable of generating nerve-force. There is no exception to this rule, but there are differences in the properties of certain fibres. The nerves generally, for example, receive direct impressions, the motor filaments conducting these to the muscles and the sensory filaments conveying the impressions to the centres. These fibres also conduct the force generated by the nerve-centres. But there are many fibres, such as those composing the white matter of the encephalon and the spinal cord, that are insensible to direct irritation, while they convey to the centres impressions made by the sensitive nerves and conduct to the motor nerves the stimulus generated by nerve-cells.

Structure of the Nerves.—There are few anatomical elements that present greater variations in size and appearance than the nerve-fibres. Certain fibres found in the course of the nerves between the muscles are as large as $\frac{1}{1250}$ of an inch, have dark borders, and possess three well-marked structures, viz., a tubular membrane, medullary contents, and an axial band; others, with the same structure, are only $\frac{1}{25000}$ of an inch in diameter; others have only the medullary covering and the axial band; and others present the axial band alone. Most of these anatomical elements have essentially the same physiological conducting properties; the variations in their structure depending upon differences in their anatomical relations. In view of these facts, it will be convenient to adopt some anatomical classification of the fibres.

In the most simple classification of the nerve-fibres, they are divided into two groups; one embracing those fibres which have the conducting element alone, and the other presenting this element surrounded by certain accessory structures. In the course of the nerves, the simple fibres are the exception, and the other variety is the rule; but, as the nerves are followed to their terminations in muscles or sensitive parts, or are traced to their origin in the nerve-centres, we find that they lose one or another of their adventitious elements. These two varieties we shall term: 1. The medullated fibres, and 2. The simple, or non-medullated fibres.

Medullated Nerve-fibres.—These fibres are so called by French and German writers because, in addition to the axis-cylinder, or conducting element, they contain, enclosed in a tubular sheath, a soft substance called the medulla. This substance is strongly refractive and gives the nerves a peculiar appearance under the microscope, from which they are sometimes called the dark-bordered nerve-fibres. As the whole substance of the fibre is enclosed in a tubular membrane, these are frequently spoken of as nerve-tubes.

If the nerves be examined while perfectly fresh and unchanged, their anatomical elements appear in the form of simple fibres with strongly-accentuated borders. The diameter of these fibres is from $\frac{1}{2500}$ to $\frac{1}{1700}$ of an inch. To observe the fibres in this way, it is necessary to take a nerve from an animal just killed and examine it without delay. In a very short time, the borders become darker and the fibre assumes an entirely different appearance. By the use of certain reagents, it can be demonstrated that a medullated nerve-fibre is composed of three distinct portions; viz., a homogeneous sheath, a semi-fluid matter contained in the sheath, and a delicate central band.

The tubular sheath of the nerve-fibres is a somewhat elastic, homogeneous membrane, never striated or fibrillated, and presenting generally oval nuclei, with their long diameter in the direction of the tube. This is sometimes called the neurilemma, a name, however, which is more generally applied to another membrane. It is sometimes spoken of, also, as the "limiting membrane of Valentin," or "the sheath of Schwann." In its chemical and general properties, this membrane resembles the sarcolemma, although it is less elastic and resisting. It exists in all the medullated nerve-fibres, large and small, except those in the white portions of the encephalon and spinal cord. It is not certain that it does not exist in the small, non-medullated fibres, although its presence here has never been satisfactorily demonstrated. As we before remarked, the tubular membrane cannot be seen in the perfectly fresh nerves; and, even after they have become changed by desiccation, its demonstration requires the use of reagents. In the ordinary medullated fibres, however, it may be isolated by boiling the nerve in absolute alcohol and then in acetic acid, or by treating it with cold caustic soda. By then boiling the nerve for an instant in the caustic soda, fragments of the tube may be isolated, when they resemble the membrane forming the canals of the kidney. Another method is to treat the nerve with fuming nitric acid, afterward adding a solution of caustic potash. The fatty substance is then discharged in small drops, the central band is dissolved, and the empty sheath is seen, swollen and tinged with yellow.

The medullary substance fills the tube and surrounds the central band. This is called by various names, as myeline, white substance of Schwann, medullary sheath, nervous medulla, etc. It does not exist either at the origin of the nerves in the gray substance of the nerve-centres or at the peripheral termination of the nerves, and it is probably not an essential conducting element. When the nerves are perfectly fresh, this substance is transparent, homogeneous, and strongly refracting, like oil; but, as the nerves become altered by desiccation, the action of water, acetic acid, and various other reagents, it coagulates into an opaque, granular mass. The consistence of this substance gives to the medullated fibres a very peculiar appearance. The tubular membrane being very thin and not elastic, the white substance, by very slight pressure, is made to fill the tubes irregularly, giving them a varicose appearance, which is entirely characteristic. In examining a preparation of the nervous tissue, large drops, coagulated in irregular shapes, are seen scattered over the field and frequently fringing the divided ends of the tubes. In the white substance of the encephalon and spinal cord, where the tubular membrane is wanting, the varicose appearance of the fibres is more remarkable than in any other situation.

The axis-cylinder is, in all probability, the essential anatomical element of the nerves. It exists in all the nerves except in those termed gelatinous fibres, or fibres of Remak, which will be described hereafter. In the ordinary medullated fibres, the axis-cylinder cannot be seen in the natural condition of the tissue, because it refracts in the same manner as the medullary substance, and it cannot be demonstrated afterward, on account of the opacity of the coagulated matter. If a fresh nerve, however, be treated with strong acetic acid, the divided ends of the fibres will retract, leaving the axis-cylinder, which is but slightly affected by reagents. It then presents itself in the form of a pale, slightly-flattened band, with outlines tolerably regular, though slightly varicose at intervals, somewhat granular, and sometimes very finely striated in a longitudinal direction. This band is elastic but not very resisting. Its granules are excessively pale. What serves to distinguish it from all other portions of the nerve-fibre is its insolubility in most of the reagents employed in anatomical investigations. It is slightly swollen by acetic acid but is dissolved after prolonged boiling. If a solution of carmine be applied to the nervous tissue, the axis-cylinder only is colored. It has been remarked that the nerve-fibres treated with nitrate of silver present in the axis-cylinder well-marked transverse striations; and some observers are disposed to regard both the nerve-cells and the axes of the fibres as composed of two substances, the limits of which are marked by the regular striæ developed by the nitrate of silver. This, however, is a point of purely anatomical interest. The presence of regular and well-marked striæ in the axis-cylinder after the addition of a solution of nitrate of silver and the action of light cannot be doubted; but it has not yet been determined beyond question whether these markings be entirely artificial, or whether the axis-cylinder be really composed of two kinds of substance.

A still more important question with regard to the intimate structure of the axis-cylinder refers to the longitudinal striations. These are observed in many fibres, but they are not constant. Some authors have adopted the view that the markings are produced by fibrillæ, analogous to the fibrillæ of the muscular fibres, in all the fibres, as well as in those of the retina, the olfactory, and some of the sympathetic nerves. In the organs of special sense, there can be no doubt of the existence of fibrillæ; but this is by no means so clearly demonstrable in the general system of nerves. Still, it is necessary to take into consideration, in this connection, certain facts with regard to the origin of the nerve-fibres in the cells and their ultimate distribution in sensitive parts. In the final distribution of sensitive nerves, we shall see that the fibres break up into filaments resembling fibrillæ; and, although the fibrillated character of the poles of the nerve-cells is not unreservedly accepted by anatomists, many observers positively state that such is their structure. In the present condition of the science, we cannot do more than state that, while a fibrillated structure has perhaps been shown in the nerves of some of the lower orders of animals, its existence in man and in the mammalia is somewhat doubtful.

The diameter of the axis-cylinder is about one-half or one-third that of the tube in which it is contained. The various appearances which the nerve-fibres present under different conditions are represented in Fig. 174.

Simple, or Non-medullated Nerve-Fibres.—These fibres are found very largely distributed in the nervous system. When we come to study the structure and relations of these small fibres, which seem in many instances to be simple prolongations, without alteration, of the axis-cylinder of the medullated fibres, it will be seen that they are chiefly found in the peripheral terminations of the nerves and in the filaments of connection of the fibres with the cells. The study of the fibres in these relations constitutes the most important part, physiologically, of the anatomy of the nerves and presents the greatest difficulties in the way of direct observation; and, for these reasons, we shall treat of these questions separately, and defer, for the present, the full consideration of the non-medullated fibres.

FIG. 174.—*Nerve-fibres from the human subject; magnified 350 diameters.* (Kölliker.)

Four small fibres, of which two are varicose, one medium-sized fibre with borders of single contour, and four large fibres; of the latter, two have a double contour, and two contain granular matter.

Gelatinous Nerve-Fibres (Fibres of Remak).—These fibres are entirely different in their anatomy from either of the varieties of fibres just considered. They are found chiefly in the sympathetic system and in that particular portion of this system connected with involuntary movements. For instance, these fibres are very abundant in the gray filaments sent to parts provided with non-striated muscular fibres and endowed with undoubted motor properties; but they are not found in the white filaments of the sympathetic, which seem to be incapable of exciting movements.

There is considerable difference of opinion among physiologists with regard to the gelatinous filaments. Some are disposed to regard them as elements of connective tissue, not endowed with properties characteristic of nerves, while others consider that they are nerve-fibres, probably possessing functions distinct from those of the fibres of different structure. The latter is the view now adopted by the best anatomists. While it is certain that elements of connective tissue exist in the nerves, and that these have been mistaken for true nerve-fibres, there are in the nerves, particularly in those belonging to the great sympathetic system, fibres exactly resembling the nerve-fibres of the embryon. These are the true gelatinous nerve-fibres, or fibres of Remak. It is stated that the nerves generally have this structure up to the fifth month of intra-uterine life, and that, in the regeneration of nerves after division or injury, the new elements assume this form before they arrive at their full development.

The true gelatinous nerve-fibres present the following characters: They are flattened, with regular and sharp borders, grayish and pale, presenting numerous very fine granulations, and a number of oval, longitudinal nuclei, a characteristic which has given them the name of nucleated nerve-fibres. The diameter of the fibres is about $\frac{1}{8000}$ of an inch. The nuclei have nearly the same diameter as the fibres and are about $\frac{1}{1200}$ of an inch in length. They are finely granular and present no nucleoli. The fibres are rendered pale by the action of acetic acid, but they are slightly swollen only, and present, in this regard, a marked contrast with the elements of a connective tissue. The microscopical appearances of these fibres, which are strongly characteristic, are represented in Fig. 175.

Accessory Anatomical Elements of the Nerves.—The nerves present, in addition to the different varieties of true nerve-fibres just described, certain accessory anatomical elements common to nearly all of the tissues of the organism, such as connective tissue, blood-vessels, and perhaps lymphatics, although these have never been demonstrated, except in the nerve-centres.

Like the muscular tissue, the nerves are made up of their true anatomical elements—the nerve-fibres—held together into primitive, secondary, and tertiary bundles, and so on, in proportion to the size of the nerve. The primitive fasciculi are surrounded by a delicate membrane, described by Robin under the name of *périnèvre*, but which had been already noted by other anatomists under different names. This membrane is homogeneous or very finely granular, sometimes marked with longitudinal striæ, and possessing elongated nuclei, finely granular, from $\frac{1}{2000}$ to $\frac{1}{1000}$ of an inch in length by from $\frac{1}{8000}$ to $\frac{1}{5000}$ of an inch wide. The thickness of the membrane is from $\frac{1}{12000}$ to $\frac{1}{8000}$ of an inch. It commences at the point where the nerve-fibres emerge from the white portion of the nervous centres, and it extends to their terminal extremities, being interrupted by the ganglia in the course of the nerves. This membrane generally envelops a primitive fasciculus of fibres, branching as the bundles divide and pass from one trunk to another; but it is sometimes found surrounding single fibres. It is not usually penetrated by blood-vessels, the smallest capillaries of the nerves ramifying in its substance but seldom passing through to the individual nerve-fibres. Within the perinerve, are sometimes found elements of connective tissue, with very rarely a few capillary blood-vessels in the largest fasciculi.

FIG. 175.—*Fibres of Remak; magnified* 300 *diameters.* (Robin.) With the gelatinous fibres, are seen two of the ordinary, dark-bordered nerve-fibres.

The amount of fibrous tissue in the different nerves is very variable and depends upon the conditions to which they are subjected. In the nerves within the bony cavities, where they are entirely protected, the fibrous tissue is very scanty; but, in the nerves between muscles, we find a tolerably strong investing membrane or sheath surrounding the whole nerve and sending processes into its interior, which envelop smaller bundles of fibres. This sheath is formed of inelastic fibres, with small elastic fibres and nucleated connective-tissue fibres. These latter may be distinguished from the gelatinous nerve-fibres by the action of acetic acid, which swells and finally dissolves them, while the nerve-fibres are but slightly affected.

The late researches of Sappey have shown that the structure of the fibrous sheath of the nerves possesses certain important anatomical peculiarities. The greatest part of this membrane is composed of bundles of white inelastic tissue, interlacing in every direction; but it contains also numerous elastic fibres, adipose tissue, a net-work of arteries and veins, and "nervi-nervorum," which are to these structures what the vasa-vasorum are to the blood-vessels. The adipose tissue is constant, being found even in extremely emaciated persons.

The vascular supply to most of the nerves is rather scanty. The arteries break up into a plexus of very fine capillaries, arranged in oblong, longitudinal meshes surrounding the fasciculi of fibres; but they rarely penetrate the perinerve, and they do not usually come in contact with the ultimate nervous elements. The veins are rather more voluminous and follow the arrangement of the arteries. It is not certain that the nerves in their course contain lymphatics; at least these vessels have never been demonstrated in their substance.

Branching and Course of the Nerves.—The ultimate nerve-fibres in the course of the nerves have no connection with each other by branching or inosculation. A bundle of fibres frequently sends branches to other nerves and receives branches in the same way; but this is simply the passage of fibres from one sheath to another, the ultimate fibres themselves maintaining throughout their course their integrity and their individual physiological properties. This view with regard to the course of the fibres in the nerves is held by nearly all anatomists. The nerve-fibres do not branch or inosculate except at the point where they change their character just before their termination. The branching and inosculation of the ultimate nerve-fibres will be considered in connection with the very interesting and important question of their ultimate distribution to muscles and sensitive parts.

Mode of Termination of the Nerves in the Voluntary Muscles.—For a long time, the mode of termination of the nerve-fibres in the muscles was a question of great uncertainty; but, within the last few years, thanks to the elaborate researches of French and German anatomists, the peripheral extremities of the nerves have been so accurately described and figured, that the great question of the mode of connection between the anatomical element conducting the stimulus to the muscles and the contractile elements of the muscles themselves may be considered as definitively settled. In 1840, Doyère gave an account of the peripheral termination of the motor nerves, probably as accurate as was possible with his imperfect means of investigation; but this observation, though confirmed a few years later by Quatrefages, seems to have been lost sight of by most physiological writers. Without underestimating the value of other researches, we may state that those of Rouget represent, perhaps, the present condition of the question as well as any. The differences, however, between the most reliable observations of recent writers are nearly all unimportant; and, while future investigations may enable us to go farther in following out some of the elements of the nerve-fibres, they will, in all probability, simply extend our knowledge, without invalidating the information already acquired.

The observations of Rouget were published in 1862 and were made upon lizards, frogs, Guinea-pigs, rats, and other animals, and have been confirmed in the human subject. The tissues were taken either from the living animal or from an animal just killed, and they were examined, in some instances, without the addition of reagents; but the most satisfactory results were obtained by macerating the muscles for from six to twenty-four hours in a liquid containing $\frac{1}{1000}$ of hydrochloric acid, and adding to the preparation on the glass slide a drop of a solution of sugar in water. In preparations made in this way, it is easy to trace the course of the nerves to their termination. The following is the description given by Rouget:

"The nervous trunks and the branches of distribution generally cross the course of the muscular fibres. As regards the terminal ramifications, sometimes they meet the muscular fibres at nearly a right angle, and sometimes they are placed nearly parallel to the axis of the primitive fasciculi. Branches of distribution are detached sometimes from branches containing two or three fibres, and sometimes from isolated fibres. After a very short course these tubes divide, and may present as many as seven or eight successive divisions. Most commonly, the termination takes place either by divisions of the second or third order, or the same tube gives off, successively, divisions which pass to the adjacent primitive fasciculi and terminate here without new divisions and after a very short course. They have a less diameter than the primitive nerve-tubes, but they preserve even to the terminal extremity their double contour, and there can be demonstrated, very easily, a sheath provided with nuclei, a medullary layer, and the *axis-cylinder*. Never do we observe at the termination of the motor nerves the pale and non-medullated fibres described by Kühne and Kölliker. At the point where the tube terminates, we remark constantly a special arrangement which has no analogy with that which has been described in the batrachia by these two observers, and which Kühne believed could be extended to the higher vertebrata, to the mammalia, and to the human subject. The nerve-tube, with a double contour, preserving still a diameter of from $\frac{1}{3000}$ to $\frac{1}{2500}$ of an inch at the point where it touches the primitive fasciculus to become arrested at its surface, terminates by an expansion of the central nerve-substance, the axis-cylinder, which is in immediate contact with the contractile fibres (fibrillæ) of the primitive fasciculus. The layer of medullary substance ceases abruptly at this point, the sheath of the tube is spread out and blended with the sarcolemma; but in immediate continuity with the axis-cylinder, a layer, a plate of granular substance, from $\frac{1}{6000}$ to $\frac{1}{4000}$ of an inch in thickness, is spread out beneath the sarcolemma, on the surface of the fibrillæ, in a space generally oval and about $\frac{1}{1250}$ of an inch wide in its short diameter, and $\frac{1}{500}$ of an inch in its long diameter. This granular substance masks more or less completely, in the space which corresponds to it, the transverse striæ of the muscular fasciculus. The disk itself has exactly the granular appearance of the substance of the axis-cylinder in the vertebrata, and of that of the nerve-tubes in most of the invertebrata, especially after being treated by diluted acids. But that which essentially characterizes the terminal plates of the motor nerves is an agglomeration of nuclei observed at their site. With a low magnifying power, even, we can distinguish the point where a nerve-tube touches the primitive fasciculus to which it belongs, and ends abruptly at its surface, by a collection of from six to twelve or even sixteen nuclei which occupy the site of the terminal plate. These nuclei are distinguished by their size as well as by their form, which is less elongated than the nuclei of the muscular tissue (*connective-tissue nuclei of the primitive fasciculi*). They present, however, the most complete analogy with the nuclei of the nerve-sheath (*connective-tissue nuclei of the nerves*). They are, without any doubt, nothing else than the nuclei which, scattered throughout the entire length of the sheath, are collected in a mass at the point where the covering of the nerve-fibre is spread out and fuses with the sarcolemma of the primitive fasciculus."

There can be little if any doubt that the description just given represents the mode of termination of the nerves in the voluntary muscles in man and in the mammalia. The observations of Kölliker, who describes a plexus of pale fibres with nuclei instead of a well-defined terminal plate, were made upon frogs, and are probably correct; and Kölliker admits the accuracy of the observations of Rouget as regards reptiles, birds, and the mammalia.

Although the sensibility of the muscles is slight as compared with that of the tegumentary tissues, they undoubtedly possess nerve-fibres other than those exclusively devoted to motion. In addition to the fibres just described, Kolliker and some others have noted fibres with a different mode of termination. These Kölliker believes to be sensitive nerves, and their mode of termination has not been so definitely described as that of the fibres with terminal motor plates. We refrain from giving a very full description even of what has been observed with regard to the termination of these fibres, for future and more successful researches will probably modify the views now held with regard to this point. Kölliker states that the fibres in question are very fine, dark-bordered tubes, with a medullated sheath, which, when studied in muscular tissue rendered pale by acetic acid, may be seen to give off exceedingly fine, non-medullated fibres, which terminate in fibres of the same appearance, but provided with nuclei. It does not appear to be certain how these fibres end. Kölliker is not satisfied that the free extremities, as they appear to be, are the actual terminations; but he asserts that in some rare instances they communicate with each other. For the present this point must be considered as unsettled.

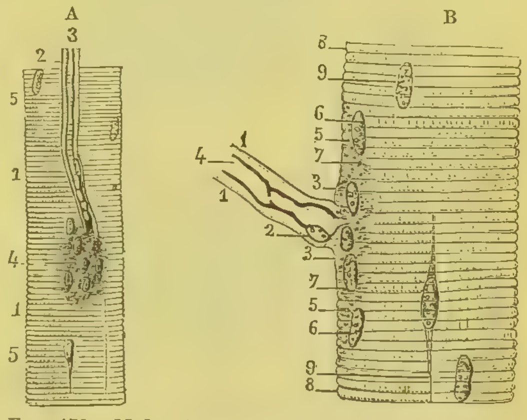


FIG. 176.—*Mode of termination of the motor nerves.* (Rouget.)

A, primitive fasciculus of the thyro-hyoid muscle of the human subject, and its nerve-tube: 1, 1, primitive muscular fasciculus; 2, nerve-tube; 3, medullary substance of the tube, which is seen extending to the terminal plate, where it disappears; 4, terminal plate situated beneath the sarcolemma, that is to say, between it and the elementary fibrillæ; 5, 5, sarcolemma.

B, primitive fasciculus of the intercostal muscle of the lizard, in which a nerve-tube terminates: 1, 1, sheath of the nerve-tube; 2, nucleus of the sheath; 3, 3, sarcolemma becoming continuous with the sheath; 4, medullary substance of the nerve-tube ceasing abruptly at the site of the terminal plate; 5, 5, terminal plate; 6, 6, nuclei of the plate; 7, 7, granular substance which forms the principal element of the terminal plate, and which is continuous with the axis-cylinder; 8, 8, undulations of the sarcolemma reproducing those of the fibrillæ; 9, 9, nuclei of the sarcolemma.

Mode of Termination of the Nerves in the Involuntary Muscular Tissue.—The nerves have not been followed out so satisfactorily in the involuntary as in the striated muscular system; and, as most if not all of the fibres are derived from the sympathetic system, which contains numerous fibres of Remak the terminations of which have not been described, it is evident that our information concerning this part of the peripheral nervous system must be incomplete. Perhaps the most remarkable of the late observations upon this point are those of Dr. Frankenhaeuser, upon the nerves of the uterus. These researches were very elaborate; but the point most interesting in this connection is that the nerves, having formed a plexus in the connective tissue, send exceedingly small fibres into the sheets or layers of muscular-fibre cells, which branch and finally go into the nucleoli of these structures. Arnold has confirmed these observations and has shown farther that, in many instances, the fine terminal nerve-fibres branch and go into the nuclei of the muscular fibres and then pass out to join with other fibres and form a plexus.

Termination of the Nerves in Glands.—The great influence which the nervous system exerts upon secretion attaches considerable interest to recent researches into the ultimate distribution of the nerves in the glands. It must be remembered, however, in these, as in all observations upon the destination of the smallest nerve-fibres, that the problem is one of the most difficult in the whole range of minute anatomy; and the results arrived at must be received with a certain amount of caution, until they shall have been amply confirmed.

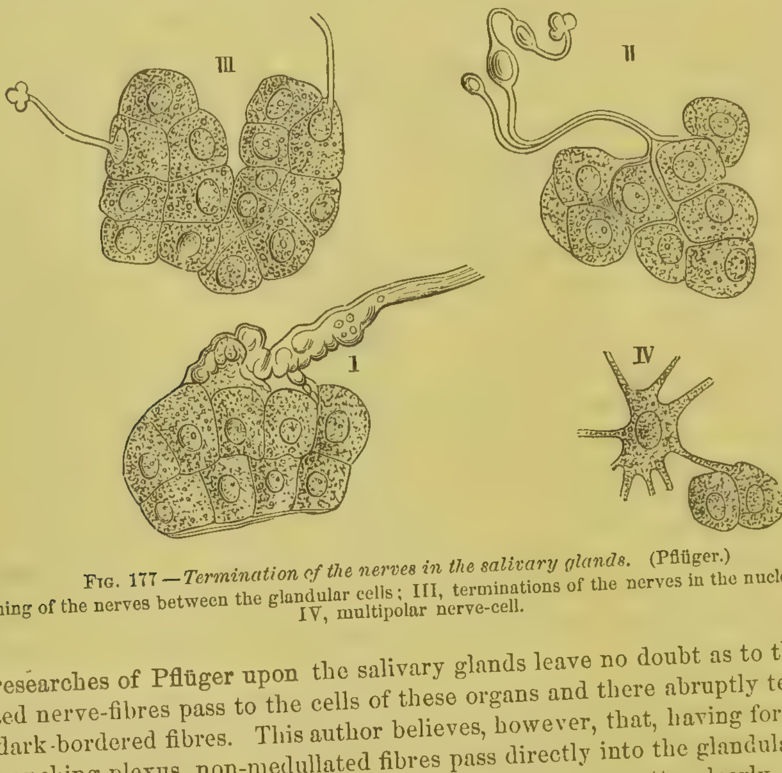


FIG. 177.—*Termination of the nerves in the salivary glands.* (Pflüger.)
I, II, branching of the nerves between the glandular cells; III, terminations of the nerves in the nuclei of the cells; IV, multipolar nerve-cell.

The researches of Pflüger upon the salivary glands leave no doubt as to the fact that medullated nerve-fibres pass to the cells of these organs and there abruptly terminate, at least as dark-bordered fibres. This author believes, however, that, having formed a more or less branching plexus, non-medullated fibres pass directly into the glandular cells, and he gives figures which seem to illustrate this arrangement pretty clearly. The same observer describes and figures multipolar cells, mixed with the glandular cells, in which some of the nerve-fibres terminate.

Modes of Termination of the Sensory Nerves.—There are undoubtedly several modes of termination of the sensitive nerves in integument and in mucous membranes, some of which have been accurately enough described, while others are still somewhat uncertain. In the first place, anatomists now recognize three varieties of corpuscular terminations, differing in their structure, probably, according to the different functions connected with sensation, with which the parts are endowed. In addition, it is probable that many sensitive nerves are connected with the hair-follicles, which are so largely distributed throughout the cutaneous surface. There are, also, terminal filaments not connected with any special organs, some of them, perhaps, ending simply in free extremities, and some connected with epithelium. There is still considerable difference of opinion among anatomists concerning all of these various points, but, with regard to the terminal corpuscles, these differences are purely anatomical, and they do not materially affect our ideas of the physiology of sensation. We do not propose, therefore, to enter fully into the discussions upon these questions, and we shall simply present what seem to be the most reasonable views of the latest and most reliable observers.

Corpuscles of Pacini, or of Vater.—These corpuscles, which were the first discovered and described in connection with the sensitive nerves, were called corpuscles of Pacini, until it was shown that they had been seen about a century and a half ago by Vater. Their actual mode of connection with the nerves, however, has only been ascertained within the last few years. The following are the measurements of these bodies and the situations in which they are found, taken from Kölliker:

In man, these corpuscles are oval or egg-shaped and measure from $\frac{1}{20}$ to $\frac{1}{6}$ of an inch in length. They are always found in the subcutaneous layer on the palms of the hands and the soles of the feet, and are most numerous on the palmar surfaces of the fingers and toes, particularly the third phalanges. In the entire hand there are about six hundred, and about the same number on the feet. They are sometimes, but not constantly, found in the following situations: The dorsal surfaces of the hands and feet, on the cutaneous nerves of the arm, the forearm and the neck, the internal pudic nerve, the intercostal nerves, all of the articular nerves of the extremities, the nerves beneath the mammary glands, the nerves of the nipples, and in the substance of the muscles of the hands and feet. They are found without exception on all of the great plexuses of the sympathetic system, in front of and by the sides of the abdominal aorta, and behind the peritoneum, particularly in the vicinity of the pancreas. They sometimes exist in the mesentery and have been observed near the coccygeal gland.

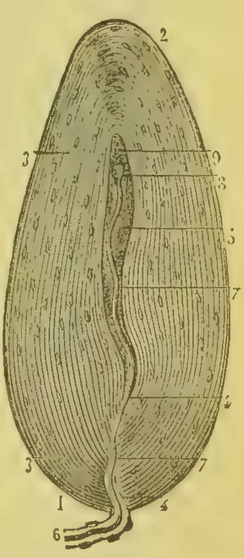


FIG. 178.—*Pacinian corpuscles.* (Sappey.)

1, base of the corpuscle; 2, apex; 3, 3, 3, substance of the corpuscle, in layers; 4, 4, nerve penetrating the corpuscle; 5, cavity of the corpuscle; 6, nerve; 7, nerve, which has lost its medullary substance and sheath; 8, termination of the nerve; 9, granular substance continuous with the nerve.

The structure of the corpuscles consists simply of several layers of connective tissue enclosing a central bulb in which is found the terminal extremity of the nerve. This bulb is finely granular, nucleated, and is regarded by most anatomists as composed of connective tissue. At the base of the corpuscle, is a pedicle formed of connective tissue surrounding a medullated nerve-fibre which penetrates the corpuscle and terminates in the central bulb.

The only really important point of discussion with reference to the structure of the nerve-fibre in the central bulb, and this is purely anatomical, is whether or not the medullary substance extend into the corpuscle itself. Probably the fibre is here reduced simply to the axis-cylinder. All anatomists agree that a single thin, flat fibre penetrates the corpuscle and terminates near its summit by a slightly-enlarged and granular extremity. The arrangement of the different anatomical elements is shown in Fig. 178.

The situation of these corpuscles beneath, instead of in the substance of the true skin, shows that they cannot be properly considered as tactile corpuscles, a name which is applied to other structures situated in the papillæ of the corium; and it is impossible to assign to them any special function connected with sensation, such as the sense of temperature, or the appreciation of pressure or weight. All that we can say with regard to them is that they constitute one of the several modes of termination of the nerves of general sensibility.

Tactile Corpuscles.—The name tactile corpuscles implies that these bodies are connected with the sense of touch; and this view is sustained by the fact that they are found almost exclusively in parts endowed to a marked degree with tactile sensibility. They are sometimes called the corpuscles of Meissner and Wagner, after the anatomists by whom they were first described. The true tactile corpuscles are found in greatest number on the palmar surfaces of the hands and fingers and the plantar surfaces of the feet and toes. They exist, also, in the skin on the backs of the hands and feet, the nipples, and a few on the anterior surface of the forearm. As we shall see when we come to describe them fully, they are situated in the substance of the papillæ of the skin, and they cannot fail to have an important function in connection with the sense of touch.

We have already treated of the general structure of the skin and have seen that the largest papillæ, measuring from $\frac{1}{250}$ to $\frac{1}{200}$ of an inch in length, are found on the hands, feet, and nipples, precisely where the tactile corpuscles are most abundant. Corpuscles do not exist in all papillæ, and they are found chiefly in those called compound. In a space of about $\frac{1}{50}$ of an inch square on the third phalanx of the index-finger, Meissner counted four hundred papillæ, in one hundred and eight of which he found tactile corpuscles, or

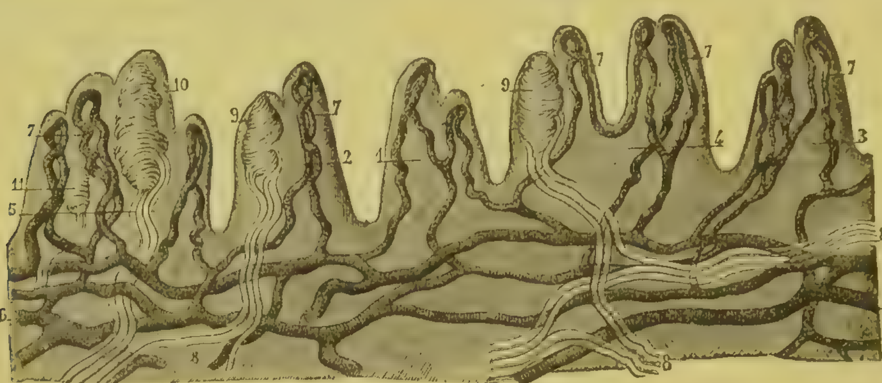


FIG. 179.—*Papillæ of the skin of the palm of the hand.* (Sappey.)

1, papilla with two vascular loops; 2, papilla with a tactile corpuscle; 3, papilla with three vascular loops; 4, 5, large compound papillæ; 6, 6, vascular net-work beneath the papillæ; 7, 7, 7, 7, vascular loops in the papillæ; 8, 8, 8, 8, nerves beneath the papillæ; 9, 9, 10, 11, tactile corpuscles.

about one in four. In the same space on the second phalanx, he found forty corpuscles; on the first phalanx, fifteen; eight on the skin of the hypothenar eminence; thirty-four on the plantar surface of the ungual phalanx of the great-toe; and seven or eight in the skin on the middle of the sole of the foot. In the skin of the forearm, the corpuscles are very rare. Kölliker states, also, that the tactile corpuscles usually occupy special papillæ, which are not provided with blood-vessels; so that the papillæ of the hand may be properly divided into vascular and nervous.

The form of the tactile corpuscles is oblong, with their long diameter in the direction of the papillæ. Their length is from $\frac{1}{350}$ to $\frac{1}{225}$ of an inch. In the palm of the hand, they are from $\frac{1}{225}$ to $\frac{1}{140}$ of an inch long, and from $\frac{1}{550}$ to $\frac{1}{500}$ of an inch in thickness. They are generally situated at the summits of the secondary eminences of the compound papillæ. According to Kölliker, the tactile corpuscles consist of a central bulb of homogeneous or slightly-granular connective-tissue substance, analogous to the central bulb of the Pacinian corpuscles, and a covering. Treated with acetic acid, the covering presents numerous elongated nuclei arranged in a circular manner, which he believes to be nuclei of connective tissue, and a few fine elastic fibres. One, two, and sometimes three or four dark-bordered nerve-fibres pass from the subcutaneous nervous plexus to the base of each corpuscle. These surround the corpuscle with two or three spiral turns, and they terminate by pale extremities at the surface of the central bulb. This arrangement is shown in Fig. 180.

Terminal Bulbs.—Under this name, a variety of corpuscles has lately been described by Krause, as existing in the conjunctiva covering the eye and in the semilunar fold, in the floor of the buccal cavity, the tongue, the glans penis, and the clitoris. They bear some analogy to the tactile corpuscles, but they are much smaller and more simple in their structure. They form simply a rounded or oblong enlargement at the ends of the nerves, which is composed of homogeneous matter, with an exceedingly delicate investment of connective tissue. They measure from $\frac{1}{1000}$ to $\frac{1}{250}$ of an inch in diameter. In the parts provided with papillæ, they are situated at the summits of the secondary elevations.

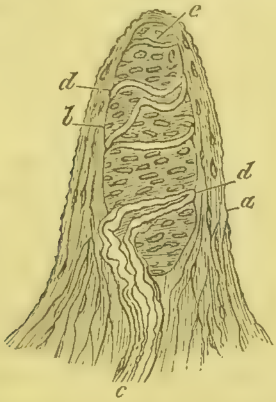


FIG. 180.—*Cutaneous papilla and tactile corpuscle.* (Kölliker.)

a, cortical layer with plasmatic cells and fine elastic fibres; *b*, tactile corpuscle, with transverse nuclei; *c*, afferent nervous branch, with its nucleated neurilemma; *d*, *d*, nerve-fibrés encircling the corpuscle; *e*, the apparent termination of one of these fibres.

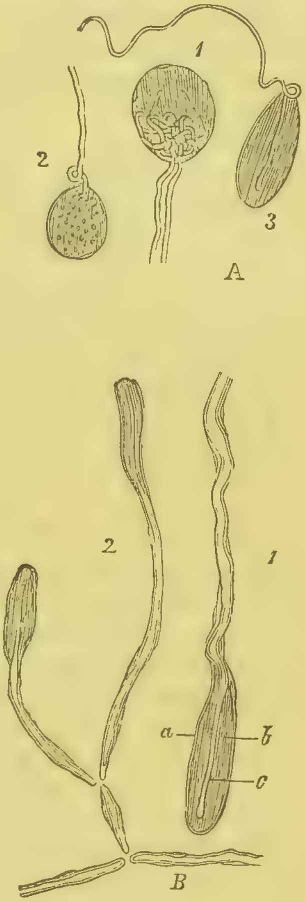


FIG. 181.—*Corpuscles of Krause.* (Ludden.)

A, three corpuscles of Krause from the conjunctiva of man, treated with acetic acid; magnified 300 diameters: 1, spherical corpuscle, with two nerve-fibres which form a knot in its interior. Portions of two pale nerve-fibres are also seen. 2, a rounded corpuscle presenting a nerve-fibre and fatty granulations in the internal bulb; 3, an elongated corpuscle with a distinct terminal fibre. In these three corpuscles, the covering, nucleated in 1 and 2, is distinguished.
B, terminal bulbs from the conjunctiva of the calf, treated with acetic acid; magnified 300 diameters: 1, extremity of a nerve-fibre with its bulb; 2, double bifurcation of a nerve-fibre, with two terminal bulbs; *a*, covering of the terminal bulbs; *b*, internal bulb; *c*, pale nerve-fibre.

The arrangement of the nerve-fibres in these corpuscles is very simple. One, two, or three medullated fibres pass from the submucous plexus to the corpuscles. The investing sheath of the fibres is here continuous with the connective-tissue covering of the corpuscle, and the nerve-fibres pass into the corpuscle, break up into two or three divisions, and terminate in convoluted or knotted coils. The nerve-fibres are medullated for a certain distance, but their terminations are generally pale. The above is one form of these corpuscles. Sometimes, however, the terminal bulbs are oblong, and sometimes but a single nerve-fibre penetrates the bulb and terminates in a simple pale filament. The principal forms of the terminal bulbs are shown in Fig. 181.

General Mode of Termination of the Sensory Nerves.—The actual termination of the sensitive nerves upon the general surface and in mucous membranes is still a question of great obscurity. Although we have arrived at a pretty definite knowledge of the sensitive corpuscles, it must be remembered that there is an immense cutaneous and mucous surface in which no corpuscles have as yet been demonstrated; and it is in these parts, endowed with what we may call general sensibility, as distinguished from the sense of touch, that we have to study the mode of termination of the nerves.

Kölliker is of the opinion that, in the immense majority of instances, the sensitive nerves terminate in some way in the hair-follicles. If this be true, it will account for the termination of the nerves in by far the greatest portion of the skin, as there are few parts in which hair-follicles do not exist; but, unfortunately, the exact mode of connection of the nerves with these follicles is not apparent. The following is all we know positively of the terminations of the nerves on the general surface:

Medullated nerve-fibres form a plexus in the deeper layers of the true skin, from which fibres, some pale and nucleated and others medullated, pass to the hair-follicles, divide into branches, penetrate into their interior, and are there lost. A certain number of fibres pass to the non-striated muscular fibres of the skin. A certain number pass to papillæ and terminate in tactile corpuscles, and others pass to papillæ that have no tactile corpuscles.

In the mucous membranes, as far as we know, the mode of termination is, in general terms, by a delicate plexus just beneath the epithelium, coming from a submucous plexus analogous to the deep cutaneous plexus. In certain membranes, we have already noted the termination in bulbs (corpuscles of Krause). In the cornea, the fibres have been followed more minutely than in any other situation, and the results of recent researches upon this subject are very remarkable. These results are so recent and unexpected, that we are hardly prepared to admit them unreservedly without full confirmation. At present we can only state that the observations of Hoyer, Lipmann, and others, confirmed in part by Kölliker, seem to show that branching nerve-fibres pass to the nucleoli of the corpuscles of the cornea and to the nucleoli of the cells of the posterior layer of epithelium.

Structure of the Nerve-centres.

A peculiar pigmentary matter in the nerve-cells and the surrounding granular substance gives to the nerve-centres a grayish color, by which they are readily distinguished from the white, or fibrous division of the nervous system. Wherever this gray matter is found, the anatomical elements of the tissue are cellular, except in the nerves formed of gray, or gelatinous fibres. Under the general division of nerve-centres, we include, anatomically at least, the gray matter of the cerebro-spinal centres, the ganglia of the roots of the spinal and certain of the cranial nerves, and the numerous ganglia of the sympathetic system. In these parts are found cells, which constitute the essential anatomical element of the tissue, granular matter resembling the contents of the cells, pale fibres originating in prolongations of the cells, elements of connective tissue, delicate membranes enveloping some of the cells, and blood-vessels. The most interesting and important of these structures, in their physiological relations, are the cells and the prolongations by which they are connected with the nerves.

Nerve-cells.—Anatomists are now pretty well agreed that the following varieties of cells exist in the nerve-centres and constitute their essential anatomical elements; viz., apolar, unipolar, bipolar, and multipolar cells. Although some have denied the existence of apolar cells, there can be little doubt of their presence in the centres in small numbers, and, as is suggested by Kölliker, they may be nerve-cells in an imperfect state of development. The nerve-cells present great differences in their size and general appearance, and some distinct varieties are found in particular portions of the nervous system and are probably connected with special functions.

The apolar cells are simply rounded bodies, with granular contents, a nucleus and nucleolus like other cells, but without any prolongations connecting them with the nerve-fibres. They have been observed in the cerebro-spinal centres, and they always exist in the sympathetic ganglia. Those who deny their existence believe that the poles have been detached in preparing specimens for examination. Unipolar cells exist in some of the lower orders of animals, but their presence in the human subject is doubtful. Bipolar cells are found in the ganglia of the posterior roots of the spinal nerves, where they are of considerable size. Smaller bipolar cells are found in the sympathetic ganglia. Multipolar cells present three or more prolongations.

Small cells, with three, and rarely four prolongations, are found in the posterior cornua of the gray matter of the spinal cord. From their situation they have been called sensory cells. They are undoubtedly found in greatest number in parts known to be endowed exclusively with sensory properties.

Large, irregularly-shaped multipolar cells, with numerous prolongations, are found chiefly in the anterior cornua of the gray matter of the spinal cord, and these have been called motor cells. They sometimes present as many as ten or twelve poles.

With all these differences in the size and form of the nerve-cells, they present tolerably uniform general characters as regards their structure and contents. Leaving out the apolar and unipolar cells, the perfectly-developed cells are of an exceedingly irregular shape, with strongly-refracting, granular contents, frequently a considerable number of pigmentary granules, and with a distinct nucleus and nucleolus. The nucleus in the adult is

FIG. 182.—*Nerve-cell from the ferruginous substance which forms the floor of the rhomboidal sinus, in man; magnified 350 diameters.* (Kölliker.)

almost invariably single, although, in very rare instances, two have been observed. Cells with multiple nuclei are often observed in young animals. The nucleoli are usually single, but there may be as many as four or five. The strongly-refracting contents, the peculiar shape, and the poles or prolongations, give to the nerve-cells an exceedingly characteristic appearance, which is represented in Fig. 182.

The diameter of the cells is as variable as their form. They usually measure from $\frac{1}{1250}$ to $\frac{1}{500}$ of an inch; but there are many of larger size, and some are smaller. The nuclei measure from $\frac{1}{2000}$ to $\frac{1}{1250}$ of an inch.

The nerve-cells are so delicate and so prone to alteration, that their study is exceedingly difficult. Sections of the nerve-centres must be prepared with great care, and they are not easily made and preserved. In the numerous anatomical investigations that have been made within the last few years, the centres have generally been hardened artificially; and almost every investigator has used different processes and reagents, which may account in a measure for the differences of opinion that now exist upon all points connected with the minute anatomy of these parts.

There is, at the present time, considerable discussion with regard to the intimate structure of the substance of the nerve-cells, their nuclei and nucleoli, and the points involved have a certain amount of physiological interest. In the first place, the transverse striæ in the axis-cylinder treated with nitrate of silver, noted by Frommann and confirmed by Grandry and others, have been observed by Grandry in the substance of the nerve-cells. While this fact, perhaps, shows that the substance contained in the cells and their prolongations is the same as the substance of the axis-cylinder, as we stated with regard to the axis-cylinder, it is possible that the markings may be entirely artificial, and that they do not demonstrate the existence of two distinct substances in the tissue.

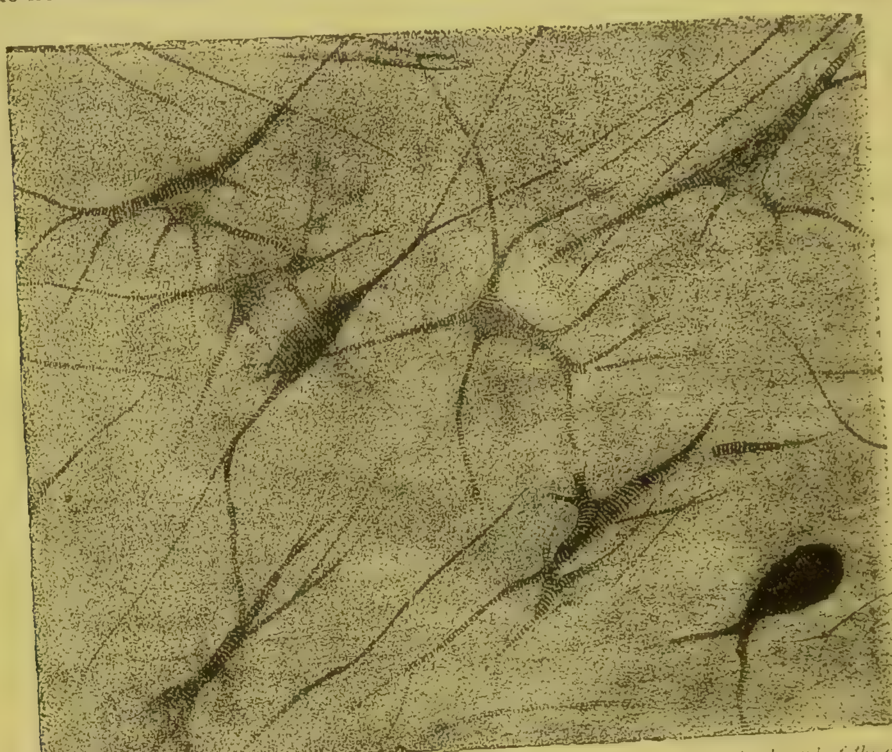


FIG. 183.—*Transverse section of the gray substance of the anterior cornua of the spinal cord of the ox, treated with nitrate of silver.* (Grandry.)

The most interesting question with regard to the structure of the nerve-cells relates to the mode of origin of their fibres or poles. Until quite recently, these have been regarded as simple prolongations of the substance of the cells; but lately the view has been advanced that the nerve-cells, in the human subject, are composed of regular fibrils continuous with the poles and starting, as it were, from the nucleoli. The fibrillation of the nerve-cells and their prolongations is figured by Schultze in an article in one of the most authoritative of the recent works on histology (Stricker); but some other eminent observers have failed to note the appearances here described, at least in the human subject and in the mammalia. With our present knowledge of the physiology of the nerve-cells, the question whether or not their substance be fibrillated has little more than an anatomical interest; but there can be no doubt that the cells in some of the lower orders of animals possess striations more or less regular. These, indeed, were described soon after the cells were discovered. While there is no anatomist who denies the fact that the substance of the cells is marked by striæ in many animals, the existence of an analogous arrangement in the human subject is still doubtful. Some anatomists, with Schultze, admit the striations but have failed to connect them with the nuclei and nucleoli. All admit that they are demonstrated with great difficulty; and, while this question is so important that it can hardly be neglected in studying the physiological anatomy of the nerve-centres, it is one concerning which it seems impossible to express a positive and definite opinion.

Connection of the Nerve-cells with the Fibres and with each other.—Although the mode of connection of the nerve-cells with the fibres and with each other is one of the most important, in its physiological bearings, of all the points connected with the minute anatomy of the nerve-centres, it is impossible, in the present state of our anatomical knowledge, to answer the questions involved in a manner entirely satisfactory. A full discussion of the different opinions and the methods of investigation that have been employed would be out of place in this work. The difficulties in the way of arriving at positive information upon these questions are the following:

1. The nerve-cells and their prolongations are so delicate and easily torn that they cannot be isolated and followed for any considerable distance, and theoretical considerations are constantly required to fill up the deficiencies in actual observation.

FIG. 184.—*Nerve-cell from the anterior cornua of the spinal cord of the calf, macerated for a short time in iodized serum; magnified 600 diameters.* (Schultze.)

a, a, axis-cylinder prolongation; *b, b, b, b*, branching prolongations.

2. In the study of sections of the nerve-centres, the parts must be hardened and afterward rendered transparent by

reagents, which must produce more or less change in the structures; and it seems an anatomical impossibility to make these sections so as to follow out the prolongations of the cells far enough to establish beyond doubt their exact relations.

These two considerations alone are sufficient to account for the uncertainty so apparent even in the most successful investigations into the anatomy of the central nervous system; and we shall content ourselves, in view of these facts, with giving a summary of what seems to be the probable relation of the cells to the fibres of origin of the nerves and to each other.

Apolar cells, if they exist at all and be not cells from which the poles have become separated, are simple, rounded bodies, lying between the fibres, with which they have no other relation than that of mere contiguity. Unipolar cells have but one prolongation, which is continuous with a nerve-fibre. It is not certain that these exist in the human subject.

Bipolar cells are found in the ganglia of the posterior roots of the spinal nerves and in some of the sympathetic ganglia. In many of the lower animals, particularly in fishes, the cells of the ganglia of the spinal nerves are simple, nucleated enlargements in the course of the sensitive nerve-fibres, and many anatomists have inferred that the same arrangement exists in man and in the mammalia; but the constitution of these ganglia in the higher classes of animals seems to be entirely different. In the first place, the roots of the spinal nerves at the ganglia are undoubtedly reënforced by the addition of new fibres, as Kölliker has shown by actual measurement, the roots being sensibly larger beyond the ganglia, while the filaments of entrance and exit have the same diameter. Direct observation upon the ganglia in man also fails to show the arrangement which is so clearly demonstrable in fishes. The cells in the posterior roots are not continuous with the fibres passing from the periphery to the cord, but they give origin to new fibres, generally two in number, which sometimes are single, and sometimes bifurcated, and which pass, in by far the greatest number of instances, if not in all, to the periphery.

The multipolar cells, with three or more prolongations, are found in all of the ganglia, but they predominate largely in the gray matter of the cerebro-spinal centres. It is the question of the exact mode of connection between these cells and the fibres of origin of the cerebro-spinal nerves and the union of the cells with each other by commissural prolongations, that presents the greatest difficulty and uncertainty. One point, which has been raised within a few years, is with regard to the character of the different poles connected with the same cell. In ordinary preparations of the central nervous system, it is impossible, even with the highest available magnifying powers, to distinguish any one pole which, in its general characters and connections, is different from the others; yet, some anatomists describe a single pole, more distinct in its outlines than the others, which does not branch and is to be regarded as an axis-cylinder. The other poles are supposed to be of a different character, not connected with the nerve-fibres, and always presenting a greater or less number of branches. These views are accepted by Schultze, who gives a figure, after Deiters, in which the contrast between the poles is represented as very marked; but, although this opinion is accepted by other high authorities, it is not easy to understand how it can be received without reserve, when it is so difficult, if not impossible, to follow out the poles, except for a very short distance.

With our present means of investigation, there seems to be no doubt with regard to the following facts: Tracing the nerve-fibres toward their origin, they are seen to lose their investing membrane as soon as they pass into the white portion of the centres, being here composed only of the medullary substance surrounding the axis-cylinder. They then penetrate the gray substance, in the form of axis-cylinders, losing here the medullary substance. In the gray substance, it is impossible to make out all of their relations distinctly, and we cannot assume, as a matter of positive demonstration, that all of them are connected with the poles of the nerve-cells. Still, it has been shown, in the gray matter of the spinal cord, that many of the fibres are actual prolongations

FIG. 185.—*Multipolar nerve-cell from the anterior cornu of the spinal cord of the ox; magnified* 200 *diameters.* (Deiters.)

a. axis-cylinder prolongation; *b, b, b, b, b, b.* branching prolongations.

of the cells, the others probably passing upward to be connected with cells in the encephalon.

Tracing the prolongations from the cells, we find that one or more of the poles branch and subdivide in the gray substance and give origin to fibres, but that these fibres do not branch after they pass into the white substance. Other poles connect the nerve-cells with each other by commissural fibres of greater or less length; but it has never been positively demonstrated that the cells are thus connected into separate and distinct groups, although this is possible.

The accompanying figure, taken from the excellent monograph on the lumbar enlarge-

FIG. 186.—*Group of cells connected with the anterior roots, as seen in a transverse section, from the anterior cornu of the sheep.* (Dean.)

A, entrance of the anterior roots into the cornu; *b, b, b, b*, cells connected by long, slender processes with the anterior roots. In this figure, almost every variety of cell-connection may be seen, with bundles of fibres crossing in every direction.

ment of the spinal cord, by Dean, shows the mode of connection between certain of the cellular prolongations and the fibres of the anterior roots, and the commissural fibres by which the cells are connected with each other.

Accessory Anatomical Elements of the Nerve-centres.—While we must regard the cells of the gray matter and the axis-cylinder of the nerves as probably the only anatomical elements concerned in innervation, there are other structures in the nervous system which it is important for us to study. These are the following: 1, Outer coverings surrounding some of the cells; 2, intercellular, granular matter; 3, peculiar corpuscles, called myelocytes; 4, connective-tissue elements; 5, blood-vessels and lymphatics.

Certain of the cells in the spinal ganglia and in the ganglia of the sympathetic system are surrounded with a nucleated covering, removed a certain distance from the cell itself, so as to be nearly twice the diameter of the cell, which is continuous with the sheath of the dark-bordered fibres. This membrane is always nucleated, and Kölliker has lately shown that it is not homogeneous, as was at one time supposed, but is composed of a layer of very delicate epithelium. The physiological significance of this covering is not apparent.

In the gray matter of the nerve-centres, there is a finely granular substance between the cells, which closely resembles the granular contents of the cells themselves. In addition to this granular matter, Robin has described new anatomical elements which he has called myelocytes. These are found in the cerebro-spinal centres, forming a layer near the boundary of the white substance, and they are particularly abundant in the cerebellum. They exist in the form of free nuclei and nucleated cells, the free nuclei being by far the more numerous. The nuclei are rounded or ovoid, with strongly-accentuated borders, are unaffected by acetic acid, finely granular, and generally without nucleoli. The cells are rounded or slightly polyhedric, pale, clear, or very slightly granular, and contain bodies similar to the free nuclei. The free nuclei are from $\frac{1}{5000}$ to $\frac{1}{4000}$ of an inch in diameter, and the cells measure from $\frac{1}{2500}$ to $\frac{1}{2000}$, and sometimes $\frac{1}{1400}$ of an inch. These elements also exist in the second layer of the retina.

There has been a great deal of discussion with regard to the presence or absence of connective-tissue elements in the cerebro-spinal centres. In the other ganglia, there has never been any doubt with regard to the presence of connective tissue in greater or less amount, and in the cerebro-spinal centres there can be hardly any question of the existence of an exceedingly delicate stroma, chiefly in the form of stellate, branching cells, serving, in a measure, to support the nervous elements.

The blood-vessels of the nerve-centres form an exceedingly graceful capillary net-work with very large meshes. The gray substance is much richer in capillaries than the white.

A remarkable peculiarity of the vascular arrangement in the cerebro-spinal centres has already been described in connection with the lymphatic system. The blood-vessels here are surrounded by what have been called perivascular canals, first described by Robin, and afterward shown by His and Robin to be radicles of the lymphatic system.

Composition of the Nervous Substance.

Our knowledge of the chemical constitution of the nervous system is, in many regards, quite unsatisfactory; but these tissues contain certain elements that have been very satisfactorily determined. The chemical characters of cholesterine, for example, have long been known to physiologists, as well as the fact that this principle is a constant constituent of the nervous substance, united in some way with the other proximate principles, so that it does not appear in a crystalline form. Since we demonstrated, in 1862, the relations of cholesterine to the processes of disassimilation, this principle has assumed its proper place as one of the most important of the products of physiological waste of the organism. The origin and function of cholesterine, with the processes for its extraction from the fluids and tissues of the body, have been fully considered under the head of excretion.

Regarding cholesterine as an excrementitious product, to be classed with principles destined simply to be eliminated from the organism, the nerve-substance proper has been found to contain the following proximate principles, the chemical properties of which have been more or less accurately determined; viz., protagon, neurine, fatty matters combined with phosphorus, and bases combined with peculiar fatty acids.

Protagon.—This principle was discovered by Liebreich and was first described in 1865. Its formula is $C_{116}H_{241}O_{22}N_4P$. It may be extracted by the following process: The cerebral substance is bruised in a mortar and afterward shaken with water and ether in a closed vessel. The mixture is then exposed to a temperature of 32° Fahr., and the ethereal layer, containing cholesterine, is removed. The insoluble mass is then extracted with alcohol (85 per cent.) at 113°, is again filtered, and is exposed to a temperature of 32°. An abundant precipitate then separates, which is washed with ether and desiccated *in vacuo*. The protagon is thus obtained in the form of a white powder. Since this principle has been described in the brain-substance, a compound analogous to if not identical with protagon has been discovered by Hermann in the blood-corpuscles. In its general and chemical characters, protagon resembles the albuminoid proximate principles; but it presents the remarkable difference, that the sulphur, which exists in many of the principles of this class, is replaced by phosphorus. It is stated by Robin that protagon is not a true proximate principle but is simply impure or imperfectly-prepared lecithene.

Neurine.—This name has been applied to a rather indefinite principle supposed to represent the albuminoid element of the nervous tissue; but its characters as a proximate constituent of the nerve-substance have never been well determined. Robin and Verdeil place neurine among the proximate principles of probable existence. According to these authors, this is the organic substance of the brain, not soluble in alcohol. When incinerated it does not leave a residue impregnated with phosphoric acid, like the cerebral fatty matter. According to more recent investigations, particularly those of Liebreich, neurine is a derivative of protagon. The neurine of Liebreich is obtained by boiling protagon for twenty-four hours in baryta-water, when there are formed the phospho-glycerate of baryta, and a new base, neurine. It is evident that this substance cannot properly be regarded as a well-determined proximate principle.

The observations of Wurtz upon the synthesis of neurine are important as a step toward the synthesis of organic nitrogenized principles, but they do not afford an example of the actual formation of a characteristic nitrogenized constituent of the nerve-tissue. They simply show that the chlorohydrate of an artificial organic compound presents crystals identical with the chlorohydrate of neurine extracted from the brain.

Cerebral Fatty Principles.—Researches into the composition of the fatty principles found in the nervous substance have been so indefinite and unsatisfactory in their results, that, even now, they possess but little physiological interest. In the earlier observations, the fats extracted from the nerve-tissue were generally combined with cholesterine. This substance has now been isolated, and the residue contains a variety of principles, which seem, under physiological conditions, to be intimately united with the nitrogenized substance, presenting one of the exceptions to the general law that fats exist in the body uncombined except with each other. In this mass of fatty matter, we can determine the presence of oleine, margarine, and stearine; but these are combined with other fats, fatty acids, etc., the remarkable peculiarity of most of which is, that they contain a certain proportion of phosphorus. These peculiar principles have received a variety of names, as they have been described more or less minutely by different observers, such as cerebrine, white and red phosphorized fat, lecithene, cerebric acid, and cerebrate of soda. The application of most of these names is very indefinite, and when we say that the substances are, in greatest part, peculiar to the nervous tissue, and that they contain phosphorus, we have stated about all that is physiologically important. Lecithene is a neutral phosphorized fat, probably composed of a number of different fatty principles, which exists, not only in the nervous substance, but in the blood, bile, and the yolk of egg. Its chemical history has no physiological interest. It is said to be identical with protagon (Robin). The same may be said of cerebric acid, the cerebrate of soda, of oleophosphoric acid and its compounds with soda and lime.

Corpora Amylacea.—Little rounded or ovoid bodies, about $\frac{1}{1800}$ of an inch in diameter, have been described by Virchow and others as existing normally in the corpora striata, the medulla oblongata, and in some other parts of the cerebro-spinal system. With regard to the actual composition of these bodies, there is considerable difference of opinion. Virchow and many others regard them as identical with starch, the granules of which they certainly resemble very closely, being of the same shape, with borders well defined, frequently presenting concentric laminæ and a hilum. When carefully treated, first with a solution of iodine and then with a little sulphuric acid, they assume a blue color. Some observers consider them as analogous to cellulose, others have supposed that they are formed of cholesterine, and others regard them as nitrogenized bodies. These points are of purely anatomical interest, and the physiological relations of these bodies are not known.

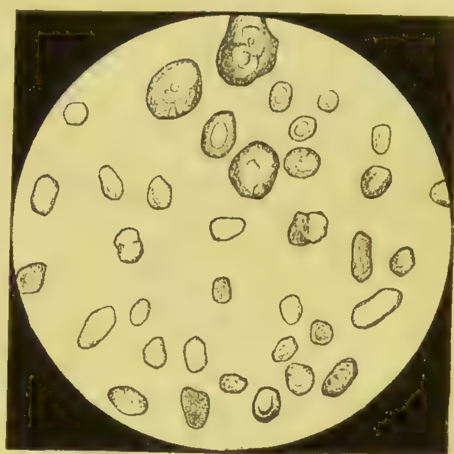


FIG. 187.—*Corpora amylacea.* (Funke.)

Regeneration of the Nervous Tissue.

We do not propose to discuss fully the question of the regeneration of nerves after section or even excision of a portion of their substance, although it is one of great pathological interest; but, in this connection, we shall refer to some experiments recently made, in which it appears that it is possible for certain of the most important of the nerve-centres to be regenerated and their function restored after extirpation.

With regard to the simple reunion of nerves after division or excision, it has long been known that this takes place in the human subject and in the inferior animals, with restoration of function. The new tissue connecting the divided extremities of the nerve seems to pass through the regular stages of development observed in the nerve-tissue of the embryon, the gelatinous fibres, or the fibres of Remak, first appearing, and these being subsequently developed into true nerve-tubes. In this process there is not a cicatrix, as in the skin or muscular tissue, but a development of new elements possessing the anatomical and physiological characters of the original structure.

A point of considerable physiological interest connected with the regeneration of the nervous tissue is involved in the recent observations of Voit upon the regeneration of the cerebral lobes after removal in a pigeon, and in those of Masius and Vanlair upon the anatomical and functional regeneration of the spinal cord in frogs.

The experiments recorded by Voit, and his deductións, are very curious and have given rise to a great deal of comment and criticism. In one observation, the cerebral lobes were removed from a young pigeon in the usual way, an operation very easily performed, and one which we practise yearly as a class-demonstration. It is particularly stated that the operation was complete, and that the entire posterior lobes were removed. Immediately after the operation, the pigeon presented the condition of stupor ordinarily observed. As he gradually recovered from this condition, he began to execute a number of mechanical movements, which it is unnecessary to detail fully, in the most extraordinary manner. The animal continued to improve, ceased the mechanical movements, and began to fly about, exhibiting timidity when approached, and, in short, seemed, after a time, to have nearly or quite returned to the normal condition. One thing, however, was remarked: the animal never took food (it was probably kept alive by stuffing, as is frequently done in such experiments). After five months, the pigeon was killed. The cranial cavity was found to be filled with a white mass, occupying the place from which the cerebrum had been removed. This mass had the consistence of the white substance of the brain and presented a perfect continuity with the cerebral peduncles, which had not been removed. It had the form of the two hemispheres, presenting a cavity filled with liquid, and a septum. The whole mass consisted of perfect primitive fibres of double contour, and, in their meshes, ganglionic cells. This observation is certainly one of the most remarkable on record, and, from the extraordinary character of its results, it would hardly be accepted for a moment, but for the established reputation of Prof. Voit. As it is, such an observation demands full confirmation. It is well known, to all who have been in the habit of extirpating the cerebral lobes, that it is absolutely necessary to remove every portion of their substance, in order to obtain uniform results, and that this is accomplished sometimes with considerable difficulty. In demonstrations to a medical class, we have frequently verified this fact, and have observed recovery, more or less complete, when but a small portion of the posterior lobes escaped. This criticism upon the remarkable observation just detailed is made by Vulpian, and its pertinence will be recognized by every practical physiologist. We have only to study the experiments first made by Flourens, to learn how, in the lower animals, a part of one of the great central ganglia may gradually assume the function of the whole, after this function has been interrupted by the first mutilation. We have cited the essential points in this observation because it has been so extensively commented upon by physiologists, but it is far from establishing the principle that a great nervous centre, like the cerebrum, may be anatomically and functionally regenerated after complete extirpation.

The general results of the experiments of Masius and Vanlair upon the regeneration of parts of the spinal cord in frogs, after loss of a small portion of its substance, show that such reparation may take place and be attended with restoration of function. The formation of cells precedes the development of fibres, and voluntary motion appears in the parts situated below the lesion, before sensation. There are no instances on record of such regeneration in the human subject or in the warm-blooded animals.

Motor and Sensory Nerves.

The physiological property of nerves which enables them to conduct to and from the centres the impressions, stimulus, force, or whatever the imponderable nervous agent may be, is one inherent in the tissue itself, belonging to no other structure, and is dependent for its continuance upon proper conditions of nutrition. So long as the nerves maintain these conditions, they retain this characteristic physiological property, which is generally known under the name of irritability.

Aside from the special senses, the sense of temperature, and the appreciation of weight, it is known to every one that, through the nerves, we appreciate what are called ordinary sensations and are enabled to execute voluntary movements. If a nerve distributed to a part endowed with sensation and the power of motion be divided, both of these properties are lost and can only be regained through a reunion of the divided nerve. Again, it is equally well known that, if such a nerve be exposed in its course and irritated, violent movements take place in the muscles to which it is distributed, and pain is appreciated, referred to parts supplied from the same source. These facts, which were fully appreciated by the ancients, show that the general system of nerves is endowed with motor and sensory properties, the question being simply whether these be inherent in the same fibres or belong to fibres physiologically distinct and derived from different parts of the central system. This question, which was solved only about half a century ago, will be the first to engage our attention.

Distinct Seat of the Motor and Sensory Properties of the Spinal Nerves.—All of the nerves that take their origin from the spinal cord are endowed with motor and sensory properties. These nerves supply the whole body, except the head and other parts receiving branches from the cranial nerves. They arise by thirty-one pairs from the sides of the spinal cord, and each nerve has an anterior and a posterior root. The anatomical differences between the two roots are that the anterior is the smaller and has no ganglion. The larger, posterior root presents a ganglionic enlargement in the intervertebral foramen. Just beyond the ganglion, the two roots coalesce and form a single trunk. The nerve-fibres in the two roots are not of the same size, the anterior fibres measuring on an average about one-fourth more than the posterior fibres. The structure of the ganglia of the posterior roots has already been considered sufficiently in detail.

It would be unprofitable to discuss the vague ideas of the older anatomists and physiologists with regard to the properties of the roots of the spinal nerves, and we can date our information upon this point from the suggestion of Alexander Walker, in 1809, that one of these roots was for sensation alone and the other for motion. It is most remarkable, however, that Walker, from purely theoretical considerations, should have stated that the posterior roots were motor and the anterior roots sensory, precisely the reverse of the truth, and should have advanced this view in a publication as late as 1844. In the work alluded to, which contains some of the most extraordinary pseudoscientific vagaries ever published, it is curious to see how near Walker came to the greatest discovery in physiology since the description of the circulation of the blood.

It is unnecessary to enlarge upon the importance of the discovery that the anterior roots of the spinal nerves are motor, and the posterior, sensory, and that the union of these two roots in the mixed nerves gives them their double properties, for we can hardly imagine a physiology of the cerebro-spinal nervous system without this fact as the starting-point. In an article published in English, in October, 1868,[1] and in French, during the same year,[2] we have given an elaborate review of the whole subject, being prompted to do so by the perusal of what purported to be an exact reprint of the original pamphlet by Charles Bell. This pamphlet was printed for private circulation, in 1811, and was never published. It has been entirely inaccessible, and its contents were only to be divined by references and quotations in the subsequent writings of Sir Charles Bell and of his brother-in-law, Mr. Shaw.

Physiological literature does not present another instance of the merit of a great discovery resting upon references to an unpublished pamphlet, which no student could possibly consult in the original, none of these references, upon close analysis, proving to be entirely distinct and satisfactory. It is not to be wondered at, therefore, that, in our study of the origin of one of the greatest discoveries of all ages, a reprint of the original memoir should be examined with the most critical care. That this reprint was correct, seemed probable from a comparison of its text with the quotations from the original to be found in the writings of Sir Charles Bell and Mr. Shaw, and from the testimony of reviewers who claimed to have compared it with the original. Within a short time, however, an authorized reprint in full, from a manuscript in the hands of the widow of the author, has appeared in the *Journal of Anatomy*.

When the only reprint of the celebrated pamphlet of Sir Charles Bell was itself excessively rare, we thought it desirable to make long quotations to indicate the ideas entertained by Bell regarding the properties of the two roots of the spinal nerves; but, now

[1] FLINT, JR., *Historical Considerations concerning the Properties of the Roots of the Spinal Nerves—Quarterly Journal of Psychological Medicine*, New York, 1868, vol. ii., p. 625, *et seq.*

[2] *Journal de l'anatomie*, Paris, 1868, tome v., p. 520, *et seq.*, and p. 575, *et seq.*

that an authorized reprint can be so readily consulted, it is only necessary to refer to this to show that Bell did not at that time regard the anterior roots as motor and the posterior roots as sensory, but that he thought that the anterior roots were for both motion and sensation and the posterior roots presided over "the secret operations of the bodily frame, or the connections which unite the parts of the body into a system."

In August, 1822, Magendie published his first experiments upon the functions of the roots of the nerves. Unlike any of the observations made by Charles Bell upon the spinal nerves, these were made upon living animals. The spinal canal was opened, and the cord, with the roots of the nerves, was exposed. The posterior roots of the lumbar and sacral nerves were then divided upon one side and the wound was united with sutures. The result of this observation was as follows:

"I thought at first that the limb corresponding to the divided nerves was entirely paralyzed; it was insensible to pricking and to the most severe pinching, it also appeared to me to be motionless; but soon, to my great surprise, I saw it move in a very marked manner, although the sensibility was still entirely extinct. A second, a third experiment, gave me exactly the same result; I commenced to regard it as probable that the posterior roots of the spinal nerves might have functions different from the anterior roots, and that they were more particularly devoted to sensibility."

The experiments in which the anterior roots were divided were no less striking:

"As in the preceding experiments, I only made the division upon one side, in order to have a term of comparison. One can conceive with what curiosity I followed the effects of this division; they were not at all doubtful, the limb was completely motionless and flaccid, while it preserved a marked sensibility. Finally, that nothing should be neglected, I divided at the same time the anterior and the posterior roots; then followed absolute loss of sensation and of motion."

From these experiments Magendie drew the following conclusions:

"I am following out my researches, and shall give a more detailed account of them in the following number; it is sufficient for me to be able to announce at present as positive, that the anterior and the posterior roots of the nerves which arise from the spinal cord have different functions, that the posterior seem more particularly devoted to sensibility, while the anterior seem more especially connected with motion."

In the second note, published in the same volume of the *Journal de physiologie* (1822), Magendie exposed and irritated the two roots of the nerves, with the following results:

"I commenced by examining in this regard the posterior roots, or the nerves of sensation. The following is the result which I observed: on pinching, pulling, or pricking these roots, the animal manifested pain; but this was not to be compared as regards intensity with that which was developed if the spinal cord were touched, even lightly, at the point of origin of the roots. Nearly every time that the posterior roots were thus stimulated, contractions were produced in the muscles to which the nerves were distributed; these contractions, however, are not well marked, and are infinitely more feeble than when the cord itself is touched. When, at the same time, a bundle of the posterior root is cut, there is produced a movement in totality in the limb to which the bundle is distributed.

"I repeated the same experiments on the anterior roots, and I obtained analogous results, but in an opposite sense; for the contractions excited by the contusion, the pricking, etc., are very forcible, and even convulsive, while the signs of sensibility are hardly visible. These facts are, then, confirmatory of those which I have announced; only they seem to establish that sensation is not exclusively in the posterior roots, any more than motion in the anterior roots. Nevertheless, a difficulty may arise. When, in the preceding experiments, the roots had been cut, they were attached to the spinal cord. Might not the disturbance communicated to the cord be the real cause either of the contractions or of the pain which the animals experienced? To remove this doubt, I repeated the experiments after having separated the roots from the cord; and I must say that, except in two animals, in which I saw contractions when I pinched or pulled the anterior and posterior roots, in all the other instances I did not observe any sensible effect of irritation of the anterior or posterior roots thus separated from the cord."

Magendie then goes on to say that, when he published the note in the preceding number of the journal, he supposed that he was the first who had thought of cutting the roots of the spinal nerves; but he was soon undeceived by a letter from Mr. Shaw, who stated that Bell had divided the roots thirteen years before. Magendie afterward received from Mr. Shaw a copy of Bell's essay ("Idea of a New Anatomy of the Brain"), and, as will be seen by the following extract, gave Bell full credit for all his observations:

"It is seen by this quotation from a work which I could not be acquainted with, inasmuch as it had not been published, that Mr. Bell, led by his ingenious ideas concerning the nervous system, was very near discovering the functions of the spinal roots; still the fact that the anterior are devoted to movement, while the posterior belong more particularly to sensation, seems to have escaped him; it is, then, to having established this fact in a positive manner that I must limit my pretensions."

Such are the experiments by which the properties of the roots of the spinal nerves were discovered. From that time, the fact took its place in science, that the posterior roots are for sensation and the anterior are for motion. Some discussion has arisen as to whether the anterior roots do not possess a certain amount of sensibility, called recurrent sensibility, and this question has engaged the attention of physiologists within a few years; but the distinct functions of the two roots have never been doubted. Before the days of anæsthetics, exposing the roots of the nerves in the dog was very laborious, and painful to the animal, and the disturbances produced by so serious an operation interfered somewhat with the effects of irritation of the different roots. But, now that the canal may be opened without pain to the animal, the experiments are much more satisfactory and have often been repeated by physiologists. We have frequently, indeed, demonstrated the properties of the roots of the nerves in public teaching.

Properties of the Posterior Roots of the Spinal Nerves.—It is unnecessary to follow out, from the date of the first experiments by Magendie to the present day, the observations that have been made from time to time upon the properties of the roots of the spinal nerves. For many years, the difficulties in operating upon animals high in the scale rendered confirmatory experiments somewhat unsatisfactory. The great German physiologist, J. Müller, showed, in experiments made upon frogs, in 1831, that irritation of the posterior roots produced no convulsive movements; but he despaired of operating satisfactorily upon warm-blooded animals. Magendie, in his later experiments, and Longet, in experiments performed upon dogs, published in 1841, showed very satisfactorily that the posterior roots were exclusively sensory, and this fact has been abundantly confirmed by more recent observations upon the higher classes of animals. We have ourselves frequently exposed and irritated the roots of the nerves in dogs in public demonstrations, in experiments upon the recurrent sensibility of the anterior roots, and in another series of observations upon the properties of the spinal cord, which will be referred to hereafter.

The remarkable anatomical peculiarity of the posterior roots, which they have in common with all of the exclusively sensitive nerves, is the presence of a ganglion. While we have no distinct idea of the function of these ganglia in connection with the transmission of impressions from the periphery to the centres, it has been shown that they have a remarkable influence upon the nutrition of the nerves after their division. Operating upon the second cervical nerves, in which the ganglia can be reached without exposing the spinal cord, Waller has demonstrated the following interesting facts:

When the roots are divided between the ganglion and the cord, the central end of the anterior root, attached to the cord, preserves its normal structure, while the peripheral end in a few days becomes degenerated, the tubes are filled with granular matter, etc., and in short, it undergoes those changes observed in all nerves separated from their centres. On the other hand, in the posterior roots, the end attached to the cord undergoes degeneration, and the peripheral end, the one to which the ganglion is attached, preserves its normal histological characters. From these experiments, which have been confirmed and somewhat extended by Bernard, it is concluded that the ganglia of the posterior roots have an influence over the nutrition of the sensitive nerves, in the same way as the centres influence the nutrition of the motor nerves with which they are connected. These points are interesting, as showing the existence of centres attached to the sensory system of nerves, which have, as far as we know, a purely trophic influence over the nerves, while the centres to which the motor nerves are attached regulate, to a certain extent, the nutrition of the nerves, and also are capable of generating nerve-force. We do not know that the ganglia of the roots of sensitive nerves have any function except that which has just been indicated.

Properties of the Anterior Roots of the Spinal Nerves.—The same experiments that demonstrated that the posterior roots of the spinal nerves are sensitive showed that the anterior roots are motor. If the two roots be exposed in an animal just killed, no convulsive movements are produced by stimulating the posterior roots; but, if the anterior roots be irritated, movements of the most violent character occur, confined to those muscles to which the filaments of the roots are distributed. There has never been any doubt upon this point since the experiments of Magendie; and it is now universally admitted by physiologists, that the motor properties of the mixed nerves are derived exclusively from their anterior roots of origin from the spinal cord. The question has arisen, however, whether the anterior roots be not also endowed with sensibility, notably less in degree than the posterior roots, but still marked and invariable. The sensibility observed in the anterior roots is abolished by section of the posterior roots; and this property, which is thought to be derived from the posterior roots, has been called recurrent sensibility.

Recurrent Sensibility.—The experimental facts with regard to the recurrent sensibility of the anterior roots of the spinal nerves are very simple. If the two roots of a spinal nerve be exposed, and if the animal be allowed to recover, by a few hours' repose, from the shock of the operation, irritation of the posterior root will produce pain and the general movements incident to it, but no localized contractions of muscles; and irritation of the anterior root will produce contraction of certain muscles and a certain amount of pain, always less, however, than the pain resulting from stimulation of the posterior roots. If the anterior root be divided, the end attached to the cord will be found completely insensible, but the peripheral end will manifest the same sensibility as the undivided root; showing that the sensory properties of the anterior roots are not derived from the cord. If the posterior root be divided, the sensibility of the anterior root is instantly abolished; showing that the sensibility of the anterior root is recurrent, being derived from the posterior root through the periphery. With regard to these facts, which were first noted by Magendie, there can be no doubt, and we ourselves verified them in a series of experiments published in 1861. Experiments have simply demonstrated the fact that the recurrent sensibility comes through the periphery, without actually showing any recurrent fibres; and division of the mixed nerve beyond the point of union of the two roots deprives the anterior root of its sensibility, showing that the recurrent fibres, if they exist, must turn back near the periphery.

The question now arises with regard to the exact mechanism of recurrent sensibility. The explanation offered by Magendie and Bernard is, that there are actually fibres returning from the posterior to the anterior roots; that these fibres are, of course, sensitive; and that irritation of the anterior roots is propagated toward the periphery and returns to the centres through the posterior roots. This explanation satisfies all of the experimental conditions, and it is farther sustained by the microscopical examinations of Schiff and of Philipeaux and Vulpian. It will be remembered that the ganglia of the posterior nerves, after division of these roots, have the remarkable power of preserving the anatomical integrity of the fibres to which they are attached. Now, it has been shown by Schiff that, after division of the posterior roots beyond the ganglia, the anterior roots contain altered fibres, which he believes come from the posterior roots and give to these roots their sensibility.

Dr. Brown-Séquard offers a different explanation of the pain developed upon irritation of the anterior roots. He believes this to be due entirely to cramp or convulsive contractions of the muscles. This may be accepted, perhaps, as a partial explanation, for there can be no doubt of the fact that violent muscular action, produced independently of volition, is more or less painful; but it does not explain the great sensibility sometimes observed when the muscular contraction is comparatively feeble. There can be hardly any doubt that the explanation offered by Magendie, and sustained by the ingenious histological observations cited above, is in the main correct.

Mode of Action of the Motor Nerves.—Having established the anatomical distinction between the motor and sensory nerves, it becomes necessary to study the differences in the mode of action of these two kinds of nervous conductors. In the first place, it is evident, taking the nerves and their roots as we find them in the organism in a normal condition, that certain fibres act from the centres to the periphery, conducting motor stimulus, while others act from the periphery to the centres, conducting sensory impressions.

As regards the motor nerves, the force, whatever it may be, generated in the centres, is conducted from the centres to the peripheral distribution of the nerves in the muscles, and is here manifested by contraction. Their mode of action, therefore, is centrifugal. When these motor filaments are divided, the connection between the parts animated by them and the centre is interrupted, and motion in these parts, in obedience to the natural stimulus, becomes impossible. But, while we cannot always induce generation of nerve-force in the centres by the direct application of any agent to them, this force may be imitated by stimulation applied to the nerve itself. A nerve that will respond to direct stimulation is said to be excitable; but this property does not extend throughout the entire conducting motor system. For example, we shall see, when we come to study the properties of the encephalon, that certain fasciculi capable of conducting the motor stimulus from the centres to the muscles are not affected by direct stimulation and seem to be inexcitable.

If a motor nerve be divided, galvanic, mechanical, or other stimulation applied to the extremity connected with the centres produces no effect; but the same stimulation applied to the extremity connected with the muscles is followed by contraction. The phenomena indicating that a nerve retains its physiological properties are always manifested at its peripheral distribution, and these do not essentially vary when the nerve is stimulated at different points in its course. For example, stimulation of the anterior roots near the cord produces contraction in those muscles to which the fibres of these roots are distributed; but the same effect follows stimulation of the nerve going to these muscles in any part of its course.

As far as their physiological action is concerned, the different nerve-fibres are entirely independent, and the relations which they bear to each other in the nervous fasciculi and in the so-called anastomoses of nerves involve simple contiguity. If we compare the nerve-force to galvanism, each individual fibre seems completely insulated; and a stimulus conducted by it to muscles never extends to the adjacent fibres. That it is the axis-cylinder which conducts and the medullary tube which insulates, it is impossible to say with positiveness; but, as we have already seen, it is more than probable that the central band is the only conducting element.

We have incidentally noted the fact that direct stimulation applied to the centres, even when the connection between these and the muscles is perfect, is generally incapable of inducing the generation of nerve-force; but the generation of a motor stimulus may be induced by an impression made upon sensitive nerves and conveyed by them to the centres. If, for example, we isolate a certain portion of the central nervous system, as the spinal cord, and leave its connections with the motor and sensitive nerves intact, these phenomena may be readily observed. An impression made upon the sensitive nerves will be conveyed to the gray matter of the cord and will induce the generation of a motor stimulus by the cells of this part, which will be conducted to the muscles and gives rise to contraction. As the stimulus, in such observations, seems to be reflected from the cord through the motor nerves to the muscles, this action has been called reflex. These phenomena constitute an important division of the physiology of the nervous system and will be fully considered by themselves.

Associated Movements.—It is well known that the action of certain muscles is with difficulty isolated by an effort of the will. This applies to sets of muscles upon one side of the body and to corresponding muscles upon the two sides. For example, it is almost impossible, without great practice, to move some of the fingers, at the same time restraining the movements of the others; and the action of certain sets of muscles of the extremities is always simultaneous. The toes, which are but little used as the foot is confined in the ordinary dress, are capable of very little independent action. It is difficult to move one eye without the other, or to make rapid rotary movements of one hand while an entirely different order of movements is executed by the other; and instances of this kind might be multiplied. In studying these associated movements, the question arises as to how far they are due to the anatomical relations of the nerves to the centres and their connections with muscles, and how far they depend upon habit and exercise. We can imagine that there may be certain sets of nerve-cells, connected with each other by commissural fibres and giving origin to motor nerves distributed to sets of muscles; an anatomical arrangement that might render a separate action of these cells impossible. The anatomy of the nerve-centres and their connection with fibres are so difficult of investigation, that demonstrative proof of the existence of such systems is impracticable; but this affords a ready explanation of the fact that we cannot, as a rule, by an effort of the will, cause only a portion of a single muscle to contract; yet some of the larger muscles receive an immense number of motor nerve-fibres which are probably connected with gray matter composed of numerous anastomosing cells.

Many of the associated movements are capable of being influenced to a surprising degree by education, of which no better example can be found than in the case of skilful performers upon certain musical instruments, such as the piano, harp, violin, and other stringed instruments. In the technical study of such instruments, not only does one hand become almost independent of the other, but very complex associated movements may be acquired. An accomplished pianist or violinist executes the different scales automatically by a single effort of the will, and frequently pianists execute at the same time scales with both hands, the action being entirely opposed to the natural association of movements. Feats of sleight of hand also show how wonderfully the muscles may be educated, and to what an extent the power of association and disassociation of movements may be acquired by long practice.

Looking at the associated movements in their relations to the mode of action of the motor nerves, it seems probable that, as a rule, the anatomical relations of the nerves are such that a motor stimulus, or an effort of the will, cannot be conducted to a portion only of a muscle, but must act upon the whole muscle, and the same is true, probably, of certain restricted sets of muscles; but the association of movements of corresponding muscles upon the two sides of the body, with the exception, perhaps, of the muscles of the eyes, is due mainly to habit and may be greatly modified by education.

Mode of Action of the Sensory Nerves.—The sensory nerve-fibres, like the fibres of the motor system, are entirely independent of each other in their action; and, in the so-called anastomoses that take place between sensory nerves, the fibres assume no new relations, except as regards contiguity.

As motor fibres convey to their peripheral distribution the stimulus engendered by an irritation applied in any portion of their course, so an impression made upon a sensitive nerve is always referred to the periphery. A familiar example of this is afforded by the very common accident of contusion of the ulnar nerve as it passes between the olecranon and the condyle of the humerus. This is attended with painful tingling of the ring and little finger and other parts to which the filaments of this nerve are distributed, without, necessarily, any pain at the point of injury. More striking examples are afforded in neuralgic affections dependent upon disease of or pressure upon the trunk of a sensitive nerve. In such cases, excision of the nerve is often practised, but no permanent relief follows unless the section be made between the affected portion of the nerve and the nerve-centres; and the pain produced by the disease is always referred to the termination of the nerve, even after it has been divided between the seat of the disease and the periphery, leaving the parts supplied by the nerve insensible to direct irritation. In cases of disease it is not unusual to note great pain in parts of the skin that are insensible to direct impressions. The explanation of this is, that the nerves are paralyzed near their terminal distribution, so that an impression made upon the skin cannot be conveyed to the sensorium; but that the trunks of the nerves still retain their conducting power and are the seat of diseased action, producing pain, which is referred by the patient to the periphery.

In multiplying examples showing the mode of action of the sensory nerves, we may refer to the sensations experienced after certain plastic operations. In the very common operation of restoring the nose by transplanting skin from the forehead, after the operation has been completed, the skin having been entirely separated and cicatrized in its new relations, the patient feels that the forehead is touched when the finger is applied to the artificial nose. After a time, however, the sensorium becomes accustomed to the new arrangement of the parts, and this deceptive feeling disappears.

There are certain curious nervous phenomena, that are not without physiological interest, presented in persons who have suffered amputations. It has been long observed that after loss of a limb the sensation of the part remains, and pain is frequently experienced, which is referred to the amputated member. Thus a patient will feel distinctly the fingers or toes after an arm or a leg has been removed, and irritation of the ends of the nerves at the stump produces sensations referred to the missing member. A few years since, we observed a very striking example of this in a soldier who had suffered amputation of the leg. While this patient was walking about on crutches, before the stump had entirely healed, upon getting up suddenly from his seat, in attempting to walk he put the stump to the ground, producing considerable injury. His explanation was, that he felt the foot perfectly, and it was necessary for him to be constantly on his guard to prevent such an accident.

A very curious fact has been observed with regard to the imaginary presence of limbs after amputation, which we have had ample opportunities of verifying. After a time the sense of possession of the lost limb becomes blunted, and it may, in some cases, entirely disappear. This may take place a few months after the amputation, or the sensations may remain in their full intensity for years. Examples are reported by Müller where the sense was undiminished thirteen, and, in one case, twenty years after amputation. In a certain number of cases, however, the sense of the intermediate part is lost, the feeling in the hand or foot, as the case may be, remaining as distinct as ever, the impression being that the limb is gradually becoming shorter. These curious facts, noted by M. Gueniot, show that the sense of the limb becoming shorter is observed in about half of the cases of amputation in which cicatrization goes on regularly; and, in these cases, the patient finally experiences a feeling as though the hand or foot were in direct contact with the stump. By careful inquiries among a large number of patients in military hospitals, we have been enabled to verify these observations in the most satisfactory manner.

General Properties of the Nerves.

Numerous experiments have been made, especially upon the cerebro-spinal nerves, with regard to their action under different kinds of stimulation, the probable nature of the nervous agent or nerve-force, the extent and duration of their excitability and sensibility, etc., which have developed facts of more or less physiological interest and importance. As far as the nerves of general sensibility are concerned, the phenomena of conduction of impressions are essentially the same in all, if we except certain variations in different nerves as regards the degree of sensibility. The motor nerves all respond in the same manner to stimulation; and it is upon this portion of the nervous system that the most important observations have been made. This being the case, it is evident that the cerebro-spinal nerves, in their behavior under the experimental conditions above mentioned, possess certain general properties, and that the functions of special nerves are to be studied, after a full consideration of these general properties, in connection with their anatomical distribution to the different organs in the economy.

The points to be considered, aside from the simple division of the nerves into motor and sensory, are as follows:

1. The conditions of excitability and sensibility of the nerves, or what is known as nervous irritability.
2. The nature of the nervous agent, or the so-called nerve-force.
3. Certain phenomena following the application of electricity to the nerves.

Nervous Irritability.—We have already alluded in a general way to what is known as nervous irritability. The term is used by physiologists to express the condition of nerves which enables them to respond to artificial stimulation, or to conduct the natural stimulus or external impressions. So long as a nerve retains this property it is said to be irritable. Of course, while in a normal condition and during life, irritability, as applied to nerves, simply means that these parts are capable of performing their peculiar functions; but, after death, for a certain time the nerves will respond to artificial stimulation; and it is to this property that the term "irritability" seems to be most applicable. At a certain time after death, varying in different classes of animals with the activity of their nutrition, the irritability of the nerves disappears. This occurs very soon in warm-blooded animals, but it is later in animals lower in the scale, so that the latter present the most favorable conditions for experimentation. Most observations upon nervous irritability, indeed, have been made upon frogs and other cold-blooded animals. Analogous facts have already been noted with regard to the muscular system, although, as we have seen, the irritability of the muscular tissue is entirely distinct from that of the nerves.

Immediately or soon after death, when the irritability of the nerves is at its maximum, they may be excited by mechanical, chemical, or galvanic stimulus, all of these agents producing contraction of the muscles to which the motor filaments are distributed. Mechanical irritation, simply pinching a portion of the nerve, for example, produces a single muscular contraction; but, if the injury to the nerve be such as to disorganize its fibres, that portion of the nerve will no longer conduct a stimulus. Among the irritants of this kind, we may cite the extremes of heat and cold. If an exposed nerve be cauterized, a vigorous muscular contraction follows. The same effect, though less marked, may be produced by the sudden application of intense cold. Among chemical reagents, there are some which excite the nerves and others which produce no effect; but these are not important from a physiological point of view. Suffice it to say, that mechanical irritation and the action of certain chemicals are capable of exciting the nerves; but that, when their action goes so far as to disorganize the fibres, the conducting power of these fibres is lost. While, however, irritation of the nerve above the point of injury has no effect, stimulation between this point and the muscles is still followed by contraction.

The most convenient method of exciting the nerves in physiological experiments is by means of electricity, a stimulus more closely resembling the nerve-force than any other, and one which may be employed without disorganizing the nerve-tissue, and which consequently admits of extended and repeated application. The action of electricity, however, with the methods of preparing the nerves and muscles for experimentation, will be fully considered under a separate head.

The irritability of the motor system is entirely distinct from that of the sensory nerves, and one may be destroyed, leaving the other intact. This follows almost as a matter of course upon the fact of the anatomical distinction between motor and sensory nerves; but it is interesting to note the limits of the irritability after death in nerves of different properties and the differences in the manner of its disappearance. The woorara-poison, a very curious agent prepared by the South-American Indians, has the remarkable property of paralyzing the motor nerves, leaving the nerves of sensation intact. This fact has been demonstrated by Bernard and others by very curious and ingenious experiments. The poison, like those of animal origin, acts most vigorously after introduction under the skin or absorption from wounds, and it produces no toxic effects when taken into the stomach, except when introduced in large quantity in fasting animals. Under the influence of this agent, an animal dies with complete paralysis of the motor system, presenting, among other phenomena, arrest of respiration. Most of the varieties of the poison affect only the motor nerves and do not influence the action of the heart; and, in animals brought completely under its influence, artificial respiration will enable the heart to continue its action, and, in some instances, if this be persisted in, recovery will take place.

FIG. 188.—*Frog prepared so as to show that woorara destroys the properties of the motor nerves.* (Bernard.) A, A, lumbar nerves; B, aorta.

The fact that the woorara-poison affects the motor nerves only has been experimentally illustrated by Bernard, taking advantage of the reflex functions of the spinal cord to show the persistence of the irritability of the sensory nerves. The most striking of these experiments is the following: A frog is prepared by exposing the nerves in the lumbar region, and then isolating the posterior extremities by applying a strong ligature, including the aorta and all the parts except the nerves; so that, practically, the only communication between the posterior extremities and the body is by the nerves. It is evident, therefore, that, if the poison be introduced under the skin of the body, acting, as it does, through the blood, it will affect all parts except the posterior extremities; for the poison acts from the periphery to the centres and must circulate in the parts to which the motor nerves are distributed. If the posterior extremities be now irritated, the impression is conveyed to the spinal cord through the sensory filaments of the lumbar nerves, which are intact; this gives rise to a stimulus, which is reflected back through the motor filaments of the same nerve, and the ordinary reflex movements are observed in the posterior extremities. This is to be expected, inasmuch as the posterior extremities have been removed from the influence of the poison. If the anterior extremities, which are completely under the influence of the poison, be now irritated, no movements are observed in these parts, but they take place, as before, in the posterior extremities. The mechanism of this action is easily understood. Reflex phenomena, consisting in the movements of muscles, may be manifested throughout the entire system, following irritation of a single part. An impression made upon the surface is conveyed to the spinal cord, and, if this be sufficiently powerful, motor stimulus may be sent through all of the anterior roots coming from the cord. The impression made upon the anterior, or poisoned extremities, is conveyed by the sensory filaments to the cord and is transmitted to the posterior extremities through their motor nerves, which are intact. The fact of the transmission of the impression from the anterior extremities to the cord shows that the poison does not affect the sensory system.

In the same way that the woorara-poison paralyzes the motor nerves, leaving the sensory system intact, other agents, as anæsthetics, will abolish the sensibility of the nerves without affecting the motor filaments.

As we have already intimated in another connection, the nerves soon lose their irritability after they have been separated from the centres. This loss of conducting power is attended with important structural changes in the nerve fibres. The tubes lose their normal appearance, and the medullary matter becomes opaque and coagulates in large drops. The axis-cylinder is not so much modified in structure, but it certainly loses its characteristic physiological properties.

The excitability of the motor nerves disappears in about four days after resection. Of course, in experiments upon this point, it is necessary to excise a portion of the nerve to prevent reunion of the divided extremities; but, when this is done, after the fourth day, galvanization of the nerve will produce no contraction in the muscles, although the latter retain their contractility, as may be shown by the application of direct irritation. This loss of irritability is gradual, and it continues, whether the nerve be exposed and stimulated from time to time or be left to itself; and the loss of excitability progresses from the centres to the periphery. In the researches of Longet upon this subject, it was found that the lower portion of the peduncles of the brain lost their irritability first, then the anterior columns of the cord, then the motor roots of the nerves, and, last of all, the branches of the nerves near their termination in the muscles.

The sensibility of the sensory nerves disappears from the periphery to the centres, as is shown in dying animals and in experiments with anæsthetics. The sensibility is lost, first in the terminal branches of the nerves, next in the trunks and in the posterior roots of the spinal nerves, and so on to the centres. We have often illustrated this fact in experiments upon the roots of the spinal nerves and in section of the large root of the fifth pair within the cranial cavity. When an animal is brought so completely under the influence of ether that the operation of opening the spinal canal may be performed without inflicting the slightest pain, the posterior roots will be found to be distinctly sensible. We have lately been in the habit, in class-demonstrations, of dividing the fifth pair in the cranium without using an anæsthetic, as the operation is instantaneous and the effects are much more striking than when the animal has been rendered insensible and is allowed to recover; but, when we have used an anæsthetic, we could never push the effects sufficiently to abolish the sensibility of the root of the nerve. In an animal brought so fully under the influence of ether that the conjunctiva, supplied with branches of the fifth, had become absolutely insensible, the instant the instrument touched the root of the nerve in the cranium, there were evidences of acute pain. Nothing could more strikingly illustrate the mode of disappearance of the sensibility of the nerves from the periphery to the centres.

The nervous irritability may be momentarily destroyed by severe shock in killing an animal. This is sometimes illustrated in preparing frogs for experiments upon the nerves; as the shock of killing the frog by decapitation, tearing off the skin, etc., abolishes the irritability of the nerves for the moment. It has been observed, also, that a galvanic shock sufficiently powerful to destroy life instantly destroys the excitability of the motor nerves.

Nerve-Force.—The so-called nervous irritability, artificially manifested by the application of a stimulus directly to the nerve-tissue, enables the nerves to conduct from the centres to the periphery a force which is generated in the gray substance. This we may call the nerve-force. Its production is one of the most remarkable of the phenomena of life; and its essence, or the exact mechanism of its generation, is one of the problems that has thus far eluded the investigations of physiologists. We know, however, that, in the operations of the nervous system, the nerves serve simply as conductors and the nerve-cells generate the nerve-force. It is evident, also, that nearly all of the so-called vital phenomena are more or less influenced and controlled through this wonderful agent; and, throughout our study of the nervous system, we shall be constantly investigating the phenomena attending the operation of nerve-force, while we are compelled to admit our ignorance of its essential nature.

Non-identity of Nerve-Force with Electricity.—When we come to study fully the action of electricity upon the nerves, we shall see that this is by far the most convenient stimulus for exciting the nervous action and one by which we closely imitate the true nerve-force. So great is the similarity, indeed, between certain of the phenomena produced by the application of electricity and those attending the physiological action of nerves, that some physiologists have regarded the nerve-cells as generators of an electric current. This hypothesis explains the nature of nerve-force, in so far as it assimilates it to a force, with the action of which, as artificially generated, we are more or less familiar. No one at the present day, however, pretends that the nerve-force has been demonstrated to be identical with any form of electricity; and the question does not now demand extended discussion.

A series of experiments made by Prévost and Dumas, in 1823, are worthy of note as showing the absence of a true electric current in nerves in action; but these have been confirmed in later years with apparatus sufficiently delicate to settle the question beyond a doubt. The most conclusive experiments upon this subject are those of Matteucci and Longet, made upon horses, at the veterinary school at Alfort. These physiologists exposed the sciatic nerves in the living animal, and, when there was evidently a conduction in both directions, as evinced by pain and muscular action, they failed to detect the slightest evidence of an electric current with the most delicate galvanometer that could be constructed. The fact of the absence of a galvanic current in nerves during their physiological action was even more strikingly illustrated by Matteucci, who demonstrated, in the electric eel, that, although the electric discharges from the peculiar organs of this animal were under the control of the nervous system and could be excited by galvanic stimulation of the proper nerves immediately after death, no galvanic current existed in these nerves during their physiological action.

When we abandon the hypothesis of the identity of nerve-force with electricity, we are compelled to admit that the agent generated by the nerve-centres is *sui generis* and not to be compared with any force known outside of living organisms or artificially produced by direct stimulation of the nerves; but we admit, nevertheless, the fact that electricity may be generated by animals, as the electric fishes, and that electric currents exist in different anatomical structures in the living body, including the nerves, under certain conditions. Our study of the nerve-force, then, leaving its essential nature unexplained, is mainly confined to a description of its characteristic phenomena.

Rapidity of Nervous Conduction.—The first rigorous estimates of the velocity of the nerve-current were made in 1850, by Helmholtz, and were applied to the motor nerves.

The important and interesting results of these experiments were arrived at by an ingenious application of the graphic method, which has since been so largely improved and extended by Marey, and their accuracy was rendered possible by the exceedingly delicate chronometric apparatus which has been devised within the last few years.

It is unnecessary to describe fully the exact methods employed by Helmholtz and by those who immediately followed in his investigations. Suffice it to say, that this distinguished physiologist and physicist constructed apparatus which, though somewhat complex, was so accurate as to leave no doubt as to the reliability of his results. Taking into account all of the disturbing conditions, and allowing for the interval of *pose*, or the length of time between the excitation of a muscle and the commencement of its contraction, he estimated the rapidity of conduction in the motor nerves of the frog at about eighty-five feet per second. The results obtained by Marey upon frogs give a much slower rate of nervous conduction. These were followed, however, by the observations of Helmholtz and Baxt upon the human subject, which are, of course, the most interesting of all.

The process devised by Marey is admirably simple. He employed, to estimate small fractions of a second, a cylinder graduated in the following manner: An ordinary tuning-fork, vibrating, say, five hundred times per second, is so arranged that a point connected with one of its arms is made to play against a strip of blackened paper. As the paper remains stationary, the point makes but a single mark; but when the paper moves, as the point vibrates, a line is produced with regular curves, every curve representing $\frac{1}{500}$ of a second. Now, if a lever be attached to a muscle and be so arranged as to mark upon the paper, moving at the same rate, the instant when contraction takes place, it is evident that the interval between two contractions produced by stimulating the nerve at different points in its course will be most accurately indicated; and, if the length of the nerve between the two points of stimulation be known, the difference in time will represent the rate of nervous conduction.

In experiments upon frogs, the leg is prepared by cutting away the muscles and bone of the thigh, leaving the nerve attached. The lever is then applied to the muscles of the leg, and the stimulation is applied successively to two points in the nerve, the distance between them being carefully measured. The results obtained in this way showed a rate of conduction of from thirty-six to forty-six feet per second; but these are not regarded by Marey as invalidating the estimates by Helmholtz, in view of the various conditions by which the rapidity of conduction is modified.

Employing the myograph of Marey, Baxt, in the laboratory of Helmholtz, has succeeded in measuring the rate of nervous conduction in the human subject. In these experiments, the swelling of the muscle during contraction was limited by enclosing the arm in a plaster-mould and noting the contraction through a small opening. By then exciting the contraction by stimulating the radial nerve successively at different distances from the muscle, the estimate was made. The rate in the human subject was thus estimated at one hundred and eleven feet per second. The latest experiments upon this subject by Helmholtz and Baxt, in which great care was taken in the adjustment of the apparatus, showed a mean of rapidity for the motor nerves, in man, of about two hundred and fifty-four feet per second. These observations were made in the summer of 1869; and the difference in the results is in part explained by the fact, which was ascertained experimentally at that time, that a high temperature increases, and a diminished temperature retards the velocity of nervous conduction. It has been farther shown by Munk, that the rate of conduction is different in different portions of the nervous trunk; the rapidity progressively increasing as the nerve approaches its termination.

Helmholtz, Du Bois-Reymond, Marey, and others, have noted certain conditions which modify the rate of nervous conduction. One of the most prominent of these, first observed by Helmholtz, is due to modifications in temperature. By a reduction of temperature, in the frog at least, the rate is very much reduced; and at 32° it is not more than one-tenth as rapid as at 60° or 70°. Marey has also noted that the rate is sensibly reduced by fatigue of the muscles.

The same principle which has led to the determination of the rate of conduction in motor nerves, viz., an estimation of the difference in time of the passage of a stimulus applied to a nerve at two points situated at a known distance from each other, has been applied to the conduction of sensations. Hirsch is quoted as having made the first attempt to resolve this question, in 1851. He employed the delicate chronometric instruments used in astronomy, and noted the difference in time between the appreciation of an impression made upon a part of the body far removed from the brain, as the toe, and an impression made upon the cheek. This process admitted of a rough estimate of about one hundred and eleven feet per second. The later and more elaborate researches of Schelske showed a rapidity of conduction by the sensory nerves of about ninety-seven feet per second.

Attempts have been made to estimate the duration of acts involving the central nervous system, such as the reflex phenomena of the spinal cord or the operations of the cerebral hemispheres. These have been partially successful, or, at least, they have shown that the reflex and the cerebral acts require a distinctly appreciable period of time. This, in itself, is an important fact; although the duration of these acts has not yet been measured with all the accuracy that could be desired. As the general result of experiments upon these points, it is found that the reflex action of the spinal cord occupies more than twelve times the period required for the transmission of stimulus or impressions through the nerves. Donders found, in experiments upon his own person, that an act of volition required one-twenty-eighth of a second, and one of simple distinction or recognition of an impression, one-twenty-fifth of a second. These estimates, however, are merely approximative; and, until they attain greater certainty, it is unnecessary to describe in detail the apparatus employed.

The general result of the various observations we have detailed upon the rate of nervous conduction as applied to the human subject is, in the first place, that this can be measured with tolerable accuracy; second, that it is in no wise to be compared with the rate of conduction of light or electricity; and, finally, that the rate in the human subject is essentially the same in the motor and sensory nerves, being, according to the most reliable estimates, about one hundred and eleven feet per second.

Action of Electricity upon the Nerves.—A great deal has been written with regard to the effects of electricity upon the nervous system, and facts elicited by experiments upon this subject are highly important in their bearing upon physiology and pathology. Still, there are numerous observations upon this subject which have but little importance, in a purely physiological sense, except that they are curious and interesting. These we do not propose to discuss elaborately; and we shall confine ourselves chiefly to those points which bear directly upon our knowledge of the properties and functions of the nerves.

The first important fact—to which we have already alluded—is, that electricity is the best means that we have of artificially exciting the nerves. Using electricity, we can regulate with exquisite nicety the degree of stimulation; we can excite the nerves long after they have ceased to respond to mechanical or chemical irritation; the effects of different currents can be noted; and, finally, this mode of stimulation produces a peculiar and interesting condition of the parts of the nerve not included between the poles of the battery. For these reasons, it seems proper to devote some consideration, in this connection, to the effects of the application of this agent to the nerves.

So long as the nerves retain their irritability, they will respond to an electrical stimulus. Experiments may be made upon the exposed nerves in living animals or in animals just killed; and, of all classes, the cold-blooded animals present the most favorable conditions, on account of the persistence of nervous and muscular irritability for a considerable time after death. Experimenters most commonly use frogs, on account of the long persistence of the irritability of their tissues and the facility with which certain portions of the nervous system can be exposed. For ordinary experiments upon the nervous conduction, the parts are prepared by detaching the posterior extremities, removing the skin, and cutting away the bone and muscles of the thigh, so as to leave the leg with the sciatic nerve attached. A frog's leg thus isolated presents a nervous trunk one or two inches in length, attached to the muscles, which will respond to the slightest stimulus. It is by experiments made upon frogs prepared in this way that most of the important facts relative to the action of electricity upon the nervous system have been developed. A form of galvanic apparatus which we have long used and found very convenient for these experiments is essentially the one described by Bernard. It consists simply of alternate copper and zinc wires wound around a piece of wood bent in the form of a horseshoe and terminating in two platinum points representing the positive and negative poles. This forms a sort of electric forceps, about eight inches long, which, when moistened with water slightly acidulated with acetic acid, will give a current of about the strength required for most experiments.

It is evident that the galvanic current may be applied to a nerve so that the direction may, in the one case, follow the course of the nerve, that is, from the centre to the periphery, and, in the other, be opposite to the course of the nerve. These currents have been called respectively the direct, or descending, and the inverse, or ascending. When the positive pole (the copper) is placed nearer the origin of the nerve, and the negative pole (the zinc), below this point in the course of the nerve, the galvanic current follows the normal direction of the motor conduction, and this is called the direct current. When the poles are reversed, and the direction of the galvanic current is from the periphery toward the centre, it is called the inverse current. It will be convenient to speak of these two currents respectively as direct and inverse, in detailing experiments upon the action of electricity upon the nerves.

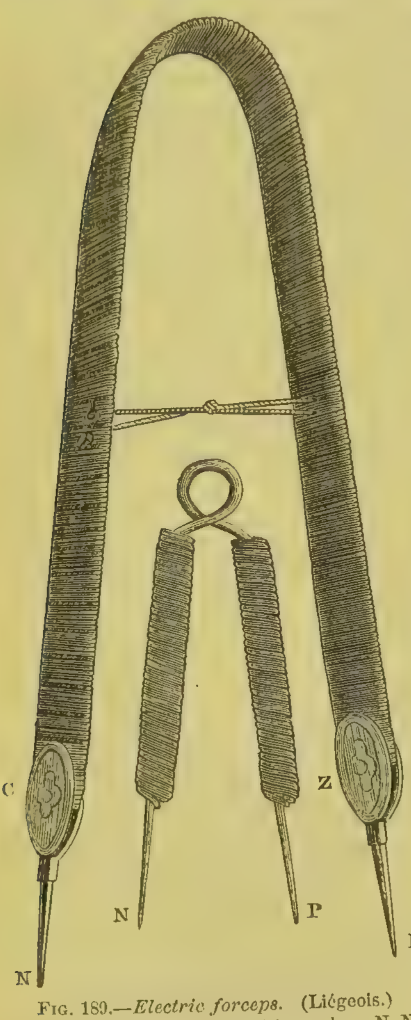


FIG. 189.—*Electric forceps.* (Liégeois.) C, copper; Z, zinc; P, P, positive poles; N, N, negative poles.

The points to be noted with regard to the effects of the application of electricity to an exposed nerve are the action of constant currents of different degrees of intensity, the phenomena observed on making and breaking the circuit, and the effects of an interrupted current.

During the passage of a feeble constant current through an exposed nerve, whatever be its direction, there are no convulsive movements and no evidences of pain. This fact has long been recognized by physiologists, who at first limited the effects of electricity upon the nerves to two periods, one at the making of the circuit and the other at its interruption. We shall see, however, that the passage of electricity through a portion of a nervous trunk produces a peculiar condition in parts of the nerve in the neighborhood of the poles of the battery, described under the name of electrotonus; but the fact that neither motion nor sensation is excited in a mixed nerve during the actual passage of a feeble constant current is not invalidated.

If a sufficiently powerful constant current be passed through a nerve, disorganization of its tissue takes place, and the nerve finally loses its excitability, as it does when bruised, ligatured, or when its structure is destroyed in any other way. It was thought by Galvani, and the idea has been adopted by Matteucci, Guérard, and Longet, that a current directed exactly across a nerve, so as to pass at right angles to its fibres, does not give rise to muscular contraction. This view is now accepted by most modern experimenters.

All who have experimented upon the action of galvanism upon the mixed nerves have noted the fact alluded to above, that the phenomena of contraction are manifested only on closing or on breaking the circuit. Take, for example, a frog's leg prepared with the nerve attached; place one pole of a feeble galvanic apparatus on the nerve and then make the connection, including a portion of the nerve in the circuit; with the mildest currents, contraction occurs only on closing the circuit, independently of the direction of the current; with currents of medium strength (Pflüger), contractions occur both at closing and opening the circuit, for currents of either direction; with strong currents, contraction occurs only at the closing of the direct current and the opening of the inverse current. After a time, however, the nervous irritability becomes somewhat enfeebled by exposure of the parts. The phenomena then observed belong to the conditions involved in the process of "dying" of the nerve. In the later stages of this condition, the phenomena may be formularized as follows:

If the sciatic nerve attached to the leg of a frog, prepared in the usual way for such experiments, be subjected to a feeble galvanic current, there is a time when muscular contraction takes place only at the instant when the circuit is made, no contraction occurring when the circuit is broken; and this occurs only with the direct current; viz., when the current flows toward the periphery, the positive pole being above, and the negative below. If the poles be reversed, so that the galvanic current flows from the periphery toward the centres (the inverse current), contraction of the muscles occurs only when the circuit is broken and none takes place when the circuit is closed. These phenomena are distinct after the irritability of the parts has become somewhat diminished by exposure or by electric stimulation of the nerve, but they may occur in perfectly fresh parts, when the galvanic current is very strong. Usually, when the nervous irritability is at its height, contractions occur both on closing and breaking the circuit; but they are more powerful on closing the circuit, for the direct current, and on breaking the circuit, for the inverse current. This fact has been noted by all modern experimenters.

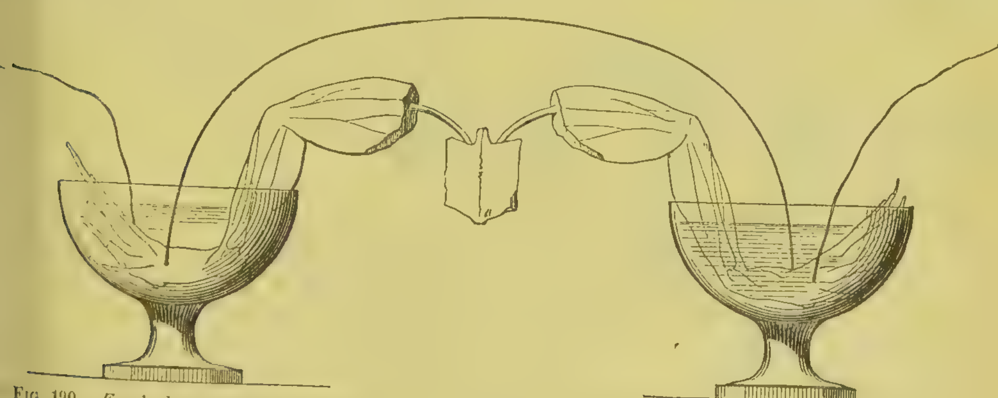


FIG. 190.—*Frog's legs prepared so as to show the contrasted action of the direct and the inverse current.* (Matteucci.)

A very simple experiment made by Matteucci strikingly illustrates the contrasted action of the direct and the inverse current. The posterior extremities of a frog are prepared so as to leave the nerves of the two sides connected together by a portion of the spinal column. The legs are then placed each one in a vessel of water, and a feeble galvanic current is passed from one glass to the other. It is evident that, with this arrangement, the current will pass through both nerves, being direct for the one and inverse for the other. In this case, if the irritability of the nerves be not too great, there will be a contraction in the leg in which the current is direct at the time of making the circuit, and the other leg will contract when the circuit is broken. This experiment has been modified by Chauveau and applied to the two facial nerves in a living horse. A Leyden jar is very feebly charged with electricity, and the two facials are exposed. The current is then passed instantaneously through both the nerves, which gives but a single stimulus and that corresponds to the time of making the circuit with the constant current. In this experiment, the current is direct for one nerve and inverse for the other, and contraction takes place only in those muscles supplied with the nerve for which the current is direct.

The muscular contraction produced by galvanic stimulation of a nerve is more vigorous the greater the extent of the nerve included between the poles of the battery. This fact has long been observed, and its accuracy is easily verified. It would naturally be expected that, the greater the amount of stimulation, the more marked would be the muscular action; and the stimulation seems to be increased in proportion to the extent of nerve through which the galvanic current is made to pass.

The irritability of a nerve, it is well known, may be exhausted by the repeated application of electricity, whatever be the direction of the current, and it is more or less completely restored by repose. It is a curious fact, in this connection, that, when the irritability of a nerve has been exhausted for the direct current, it will respond to the inverse current, and *vice versa;* and it is even more remarkable that, after the irritability has been exhausted by the direct current, it is restored more promptly by stimulation with the inverse current than by absolute repose, and *vice versa*. This phenomenon, observed by Volta, is sometimes known as "voltaic alternation." It is very strikingly illustrated in frogs prepared as above described, with the two posterior extremities, the nerves attached through a portion of the spinal cord, placed in vessels of water so that a current may be simultaneously passed through both nerves, being direct for the one and inverse for the other. As we have already seen, after a time, contraction occurs only in one leg, for which the current is direct, on making the circuit, and in the other, only on breaking the circuit. By repeatedly passing the current in this way, after a time there will be no contraction in either leg, the irritability of the nerves having become exhausted. If the poles of the battery be now reversed, so as to make the inverse current take the place of the direct, contractions with making and breaking the circuit will again occur. The irritability may again be exhausted and restored by changing the poles, and this may be repeated several times with the same preparation.

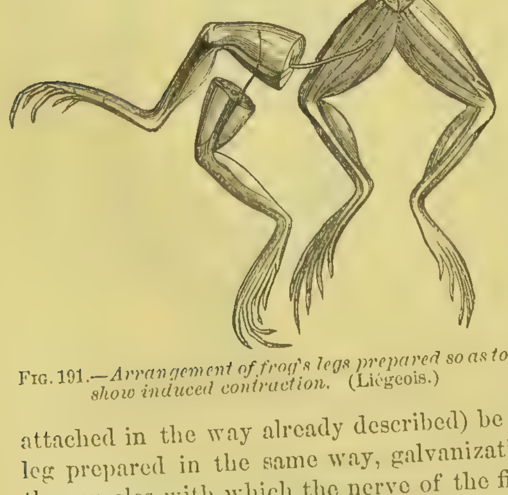


FIG. 191.—*Arrangement of frog's legs prepared so as to show induced contraction.* (Liégeois.)

Induced Muscular Contraction.—A curious phenomenon was discovered by Matteucci, in experimenting upon nervous and muscular irritability, which has been called "induced muscular contraction." It was found that, if the nerve of a galvanoscopic frog's leg (the leg prepared with the nerve attached in the way already described) be placed in contact with the muscles of another leg prepared in the same way, galvanization of the nerve giving rise to contraction of the muscles with which the nerve of the first leg is in contact will induce contraction in the muscles of both. This experiment may be extended, and contractions may thus be induced in a series of legs, the nerve of one being in contact with the muscles of another. This illustrates the great delicacy of the galvanoscopic frog's leg, as it will indicate a current due to a single muscular contraction, which does not affect an ordinary galvanometer. It is conclusively proven that the "induced contraction," as just described, is not due to an actual propagation of the galvanic current, but to a stimulus attending the muscular contraction itself, by the fact that the same phenomena occur when the first muscular contraction is induced by mechanical or chemical excitation of the nerve.

Galvanic Current from the Exterior to the Cut Surface of a Nerve.—Before we study certain phenomena presented in nerves of which a portion is subjected to the action of a constant galvanic current, it is important to note the fact that there exists in the nerves, as in the muscles, a galvanic current from the exterior to their cut surface. This fact has been noted by all who have investigated the subject of electro-physiology. It has been roughly estimated by Matteucci that the nerve-current has from one-eighth to one-tenth the intensity of the muscular current. The existence of the nerve-current has, as far as we know, no more physiological significance than the analogous fact observed in the muscular tissue. It is presented in nerves removed from the body and has no relation to their functional activity, whether in normal action or excited by artificial stimulation.

Effects of a Constant Galvanic Current upon the Nervous Irritability.—Aside from the disorganizing effect upon the nerves of a powerful constant current, which is due solely to decomposition of their substance, a feeble current has been found to exert an important influence upon the nervous irritability, according to the direction in which the current is passed. The law in accordance with which this influence is exerted is stated by Matteucci as follows:

"A continued electric current passed through a mixed nerve, the crural or the lumbar, for example, modifies the excitability of the nerve in a very different manner, according to its direction. The excitability is enfeebled by the passage of the direct current, and, on the contrary, it is preserved and augmented, at least within certain limits, by the inverse current. The time necessary in order that the current shall produce this modification is proportionate to the degree of excitability of the nerve and in inverse ratio to the intensity of the current. After the breaking of the circuit, the modification of the nerve tends to cease at a period that is short in proportion as the excitability of the nerve is great and the intensity of the current is feeble. This proposition explains the difference in the electro-physiological effects of the continued current according to its direction, and the well-known phenomenon of voltaic alternations."

This law has been carefully studied and formularized, as above, by Matteucci, but its discovery is attributed by physiological writers to Pfaff. After a time, varying with the excitability of the nerve and the intensity of the current, the direct current will destroy the nervous irritability, but this may be restored by repose, or more quickly by the passage of an inverse current. If the inverse current be passed first for a few seconds, a contraction follows the breaking of the circuit; and this contraction, within certain limits, is more vigorous the longer the current is passed. At the same time, the prolonged passage of the inverse current increases the excitability of the nerve for any kind of stimulus. When the inverse current has been passed through the nerves for several hours, breaking of the circuit is followed by very violent contraction and a tetanic condition of the muscles, enduring for several seconds.

Electrotonus, Anelectrotonus, and Catelectrotonus.

Many years ago, Du Bois-Reymond discovered the curious and interesting fact that, when a constant galvanic current is passed through a portion of a freshly-prepared nerve, those parts of the nerve not included between the poles are brought into a peculiar condition. While in this state, the nerve will deflect the needle of a delicate galvanometer, and its excitability is modified. The deflection of the needle, in this instance, is not due to the normal nerve-current, for it occurs when the galvanometer is applied to the surface of the nerve only. It is due to an electric tension of the entire nerve, induced by the passage of a current through a portion of its extent. This condition is called electrotonus. The phenomena thus produced have been most elaborately studied by Pflüger, who farther recognized a peculiar condition of that portion of the nerve near the anode, or positive pole, differing from the condition of the nerve near the cathode, or negative pole. Near the anode, the excitability of the nerve is diminished, and this condition has been called anelectrotonus. Near the cathode, the excitability is increased, and this condition has been called catelectrotonus.

These varied phenomena have been the subject of extended investigation by electro-physiologists; and, although they are not to be ranked among the physiological properties of the nerves, they have considerable pathological and therapeutical importance. It is well known, for example, that electricity is one of the most efficient agents at our command for the restoration of the functions of nerves affected with disease; and the constant current has, particularly of late, been extensively and successfully used as a therapeutical agent. The constant current, in restoring the normal condition of nerves, must influence, not only that portion included between the poles of the battery, but the entire nerve; and the electrotonic condition, with its modifications, explains how this result may be obtained. Undoubtedly the sensory nerves are affected as well as the motor, although we have as yet but little positive information upon this point. A knowledge of the fact that the constant current diminishes the excitability of the nerve near the anode (anelectrotonus) and increases it near the cathode (catelectrotonus) may become important in determining the direction of the current to be employed in different cases of disease.

In the present condition of the subject of electro-physiology, it will be unnecessary to do more than to indicate, as clearly and simply as possible, the laws of the phenomena attending the passage of a constant current through nerves, as far as they have been definitively ascertained.

The phenomena of electrotonus are very simple; and it is only when we attempt to construct a theory to account for these phenomena that the subject becomes obscure. Suppose, for example, that a nerve be exposed in a living animal or in one just killed, and a galvanic current be applied from a Grove's battery, in which about twelve square inches of zinc are exposed to the action of a liquid containing one part of ordinary sulphuric acid to eight of water. A delicate galvanometer applied to the nerve either above or below the poles will indicate a decided current, much more intense than the tranquil nerve-current between the exterior and the cut surface. This electrotonic condition exists so long as the galvanic current is continued; and, as has been shown by Matteucci in operating upon the higher animals—rabbits, dogs, fowls, and sheep—when the galvanic current has been sufficiently powerful and prolonged, the electrotonic condition persists for a certain time after the stimulus has ceased. As we have seen that the muscular contraction following galvanic stimulation of a nerve is powerful in proportion to the extent of nerve included between the poles of the battery, so the electrotonic condition increases in intensity with the length of the nerve subjected to the constant current; provided, always, that the strength of the current be slightly increased to compensate the enfeebling action due to the resistance in the increased length of the circuit.

We do not propose to discuss fully the various theories that have been advanced in explanation of the phenomena of electrotonus. Matteucci has made a series of interesting observations upon conductors formed of very fine wires, one of platinum and the other of amalgamated zinc, covered with cotton thread soaked in a neutral solution of sulphate of zinc. The experiments were then arranged so as to operate first with the platinum wire and afterward with the zinc, by passing a galvanic current through a small portion of the conductor, in the same way as it is passed through a portion of a nerve. He found that in this way he could produce a strong electrotonic current in the platinum wire, even at a distance of more than three feet from the electrodes, while no such current was observed in the zinc. He remarks that in the platinum wire "secondary polarities" are produced very powerfully and rapidly, while these are not developed in the zinc. From these experiments alone, it might seem that the phenomena of electrotonus are to be explained entirely by the physical properties of the nerves as conductors of electricity; but various observations on the nerves under different conditions have conclusively proven the contrary. All observers are agreed that the electrotonic condition is marked in proportion to the excitability of the nerve, and it is either entirely absent or extremely feeble in nerves that are dead or have lost their irritability. If a strong ligature be applied to the extra-polar portion of the nerve, or if the nerve be divided and the cut ends be brought in contact with each other, the electrotonic condition is either not observed or is very feeble. These facts show conclusively that the phenomena of electrotonus depend upon the physiological integrity of nerves. A dead nerve, or one that has been divided or strongly ligatured, may present these phenomena under the stimulation of a very powerful current (and then only to a slight degree), when the condition depends upon the purely physical properties of the nerve as a conductor; but there is no comparison between these phenomena and those observed in nerves that retain their physiological properties. Were it otherwise, how could the physiological properties of a diseased nerve be restored throughout its whole extent by a constant current passed through a restricted portion, when the excitability of the nerve is only manifested at the closing or opening of the circuit?

Anelectrotonus and Catelectrotonus.—It is interesting to note that, when a portion of a nerve is subjected to a moderately powerful constant current, the conditions of the extra-polar portions corresponding to the two poles of the battery are entirely different. Near the positive pole, or anode, the excitability of the nerve and the rate of nervous conduction are diminished. If, however, we have a galvanometer applied to this portion of the nerve, its electromotive power, measured by the deflection of the galvanometric needle, is increased. On the other hand, near the negative pole, or cathode, the excitability of the nerve is increased, as well as the rate of nervous conduction; but the electromotive power is diminished. These facts, at least so far as they relate to the increase of the excitability of the nerve near the cathode and its diminution near the anode, are partially explained by Matteucci upon purely physical principles, depending upon the electrolytic action of the current, as is shown by the following experiment:

Two cups are filled, the one with a very feebly alkaline solution, and the other with an equally weak acid fluid. A number of galvanoscopic frogs' legs are then rapidly prepared, of which one-half the number is plunged in the alkaline and one-half, in the acid fluid, for from thirty seconds to one or two minutes. The parts are then removed from the liquids and are carefully washed and dried in bibulous paper. By touching the nerves with a strong solution of common salt, which is a powerful excitant for the nervous irritability, the nerves that had been exposed to the alkaline solution produced more powerful and prompt contractions than those exposed to the acid. Now, the electrolytic action of a constant current tends to the accumulation of hydrogen and an alkali near the cathode, and of oxygen and an acid near the anode; and by this fact, Matteucci explains the increase of excitability in catelectrotonus and the diminished excitability in anelectrotonus. As regards this question, we have only to say, as in the case of general electrotonus, that the conditions are susceptible of a partial explanation upon purely physical grounds; but precisely how far the unexplained physiological properties of the nerves are involved, it is impossible to say.

Neutral Point.—The anelectrotonic condition, on the one hand, and the catelectrotonic condition at the other pole of the battery, are marked in extra-polar portions of the nerve and are to be recognized, as well, in that portion through which the current is passing; but, between the poles, is a point where these conditions meet, as it were, and where the excitability is unchanged. This has been called the neutral point. When the galvanic current is of moderate strength, the neutral point is about half-way between the poles. "When a weak current is used, the neutral point approaches the positive pole, while in a strong current, it approaches the negative pole. In other words, in a weak current the negative pole rules over a wider territory than the positive pole, whereas in a strong current the positive pole prevails." (Rutherford.)

Negative Variation.—There remains to be considered one curious phenomenon, discovered by Du Bois-Reymond, which depends upon the action of a rapidly-interrupted current applied to an excitable nerve. If a galvanometer be applied to a living nerve so as to indicate by its deviation the normal, or tranquil nerve-current, a rapidly-interrupted current of electricity passed through a portion of the nerve, it is well known, produces a tetanic condition of the muscles. If we now watch the needle of the galvanometer, it will be observed to retrograde and will finally return to zero, indicating that the proper nerve-current has been overcome. This will be observed to a slight degree under the influence of mechanical or chemical stimulation of the nerve, the proper nerve-current being diminished, but generally not abolished. This variation of the needle under the influence of the tetanic condition has been called negative variation. We do not yet know that it has any important physiological or pathological significance.

CHAPTER XVIII.

SPINAL NERVES—MOTOR CRANIAL NERVES.

Special nerves coming from the spinal cord—Cranial nerves—Anatomical classification—Physiological classification—Motor oculi communis (third nerve)—Physiological anatomy—Properties and functions—Influence upon the movements of the iris—Patheticus, or trochlearis (fourth nerve)—Physiological anatomy—Properties and functions—Motor oculi externus, or abducens (sixth nerve)—Physiological anatomy—Properties and functions—Motor nerves of the face—Nerve of mastication (the small, or motor root of the fifth)—Physiological anatomy—Deep origin—Distribution—Properties and functions of the nerve of mastication—Facial nerve, or nerve of expression (the portio dura of the seventh)—Physiological anatomy—Intermediary nerve of Wrisberg—Decussation of the fibres of origin of the facial—Alternate paralysis—Course and distribution of the facial—Anastomoses with sensitive nerves—Properties and functions of the facial—Functions of the branches of the facial within the aqueduct of Fallopius—Functions of the chorda tympani—Influence of various branches of the facial upon the movements of the palate and uvula—Functions of the external branches of the facial—Spinal accessory nerve (third division of the eighth)—Physiological anatomy—Properties and functions of the spinal accessory—Functions of the internal branch from the spinal accessory to the pneumogastric—Influence of the spinal accessory upon the heart—Functions of the external, or muscular branch of the spinal accessory—Sublingual, or hypoglossal nerve (ninth)—Physiological anatomy—Properties and functions of the sublingual—Glosso-labial paralysis.

Spinal Nerves.

With a thorough knowledge of the general properties of the nerves belonging to the cerebro-spinal system, the functions of most of the special nerves are apparent simply from their anatomical relations. This is especially true of the spinal nerves. These, in general terms, are distributed to the muscles of the trunk and extremities, to the sphincters and the integument covering these parts, the posterior segment of the head, and a portion of the mucous membranes. It is evident, therefore, that an account of the exact function of each nervous branch would necessitate a full description, not only of the nerves, but of the muscles of the body, which is manifestly within the scope only of elaborate treatises on descriptive anatomy. It is sufficient to indicate, in this connection, that there are thirty-one pairs of spinal nerves; eight cervical, twelve dorsal, five lumbar, five sacral, and one coccygeal. Each nerve arises from the spinal cord by an anterior (motor) and a posterior (sensory) root; the posterior roots being the larger, and each having a ganglion. Immediately beyond the ganglion, the two roots unite into a single mixed nerve, which passes out of the spinal canal by the intervertebral foramen. The nerve thus constituted is endowed with both motor and sensory properties. It divides outside of the spinal canal into two branches, anterior and posterior, both containing motor and sensory filaments, which are distributed respectively to the anterior and the posterior parts of the body. The anterior branches are the larger, and they supply the limbs and all parts in front of the spinal column.

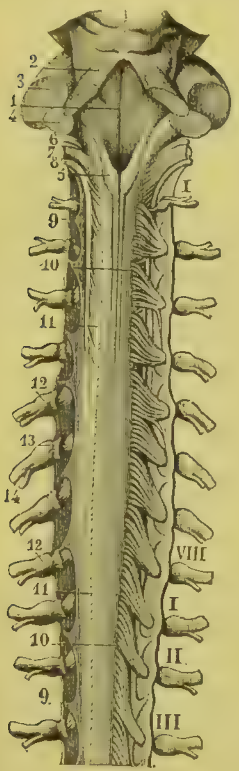


FIG. 192.—*Cervical portion of the spinal cord.* (Hirschfeld.)

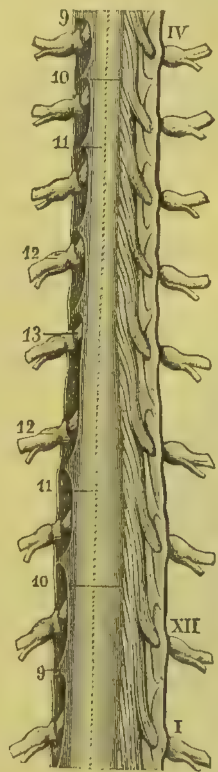


FIG. 193.—*Dorsal portion of the spinal cord.* (Hirschfeld).

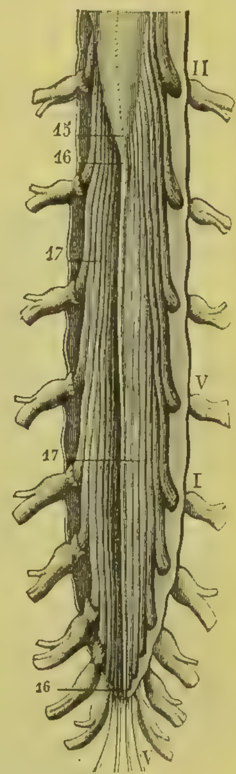


FIG. 194.—*Inferior portion of the spinal cord, and cauda equina.* (Hirschfeld.)

1, antero-inferior wall of the fourth ventricle; 2, superior peduncle of the cerebellum; 3, middle peduncle of the cerebellum; 4, inferior peduncle of the cerebellum; 5, inferior portion of the posterior median columns of the cord; 6, glosso-pharyngeal nerve; 7, pneumogastric; 8, spinal accessory nerve; 9, 9, 9, 9, dentated ligament; 10, 10, 10, 10, *posterior roots of the spinal nerves*; 11, 11, 11, 11, *posterior lateral groove*; 12, 12, 12, 12, *ganglia of the posterior roots of the nerves*; 13, 13, *anterior roots of the nerves*; 14, *division of the nerves into two branches*; 15, lower extremity of the cord; 16, 16, coccygeal ligament; 17, 17, cauda equina; I—VIII, *cervical nerves*; I, II, III, IV—XII, *dorsal nerves*; I, II—V, *lumbar nerves*; I—V, *sacral nerves*.

The anterior branches of the four upper cervical nerves form the cervical plexus, and the four inferior cervical nerves, with the first dorsal, form the brachial plexus. The anterior branches of the dorsal nerves, with the exception of the first, supply the walls of the chest and abdomen. These nerves go directly to their distribution, and do not first form a plexus, like most of the other spinal nerves. The anterior branches of the four upper lumbar nerves form the lumbar plexus. The anterior branch of the fifth lumbar nerve and a branch from the fourth unite with the anterior branch of the first sacral, forming the lumbo-sacral nerve, and enter into the sacral plexus. The three upper anterior sacral nerves with a branch from the fourth form the sacral plexus. The greatest portion of the fourth anterior sacral is distributed to the pelvic viscera and the muscles of the anus. The fifth anterior sacral and the coccygeal are distributed about the coccyx.

The posterior branches of the spinal nerves are very simple in their distribution. With one or two exceptions, which have no great physiological importance, these nerves pass backward from the main trunk, divide into two branches, external and internal, and their filaments of distribution go to the muscles and integument behind the spinal column.

It is farther important to note, as we shall have occasion to do more particularly in connection with the great sympathetic nerve, that all of the cerebro-spinal nerves anastomose with the sympathetic. This anatomical connection between the two systems of nerves has great physiological interest.

Cranial Nerves.

The nerves which pass out from the cranial cavity present certain differences, in their arrangement and general properties, from the ordinary spinal nerves. As we have seen, the spinal nerves are exceedingly simple, each one being formed by the union of a motor and a sensory root. The function of most of them follows as a matter of course when we understand their general properties and anatomical distribution. Many of the cranial nerves, however, are peculiar, either as regards their general properties or in their distribution to parts concerned in special functions. In some of these nerves, the most important facts concerning their distribution have been ascertained only by physiological experimentation, and their anatomy is inseparably connected with their physiology. It would be desirable, if it were possible, to classify these nerves with reference strictly to their properties and functions; but this can be done only to a certain extent, and we must adopt as a basis those divisions recognized in the best works upon anatomy.

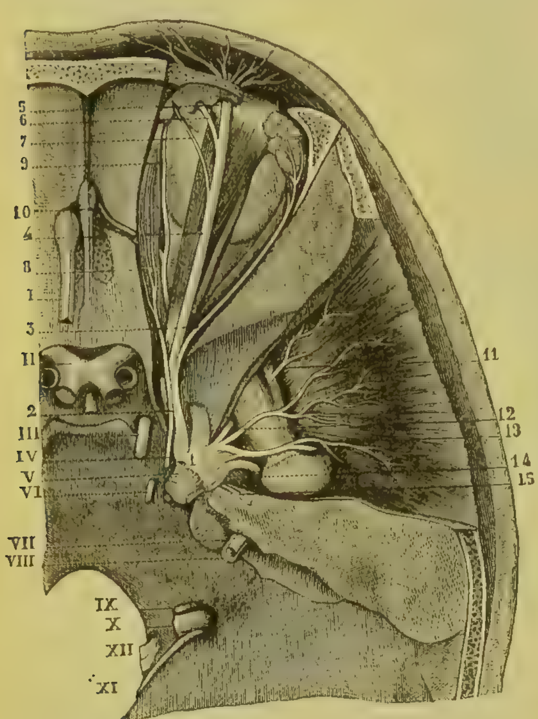


FIG. 195.—*Roots of the cranial nerves.* (Hirschfeld.)

I. First pair; olfactory.
II. Second pair; optic.
III. Third pair; motor oculi communis.
IV. Fourth pair; patheticus.
V. Fifth pair; nerve of mastication and trifacial.
VI. Sixth pair; motor oculi externus.
VII. Facial. } Seventh pair.
VIII. Auditory. }
IX. Glosso-pharyngeal. }
X. Pneumogastric. } Eighth pair.
XI. Spinal accessory. }
XII. Ninth pair; sublingual.
The numbers 1 to 15 refer to branches which will be described hereafter.

The two classifications of the cranial nerves adopted by most anatomists are the arrangements of Willis and of Sömmerring. The first of these is the more common, and in it the nerves are numbered from before backward, in the order in which they pass out of the skull, making nine pairs.

Anatomical Classification of the Cranial Nerves.

First Pair.—Olfactory; the special nerve of smell.

Second Pair.—Optic; the special nerve of sight.

Third Pair.—Motor oculi communis; a motor nerve distributed to all of the muscles of the eyeball, except the external rectus and the superior oblique, to the iris, and to the levator palpebræ.

Fourth Pair.—Patheticus, or trochlearis; a motor nerve sent to the superior oblique muscle of the eye.

Fifth Pair.—A small motor root (nerve of mastication), distributed to the muscles of mastication, and a large root (trifacial), the nerve of general sensibility of the face.

Sixth Pair.—Motor oculi externus, or abducens; a motor nerve passing to the external rectus muscle of the eye.

Seventh Pair.—Portio mollis, or auditory, a special nerve of hearing; and the portio dura, or facial, a motor nerve distributed to the superficial muscles of the face.

Eighth Pair.—Glosso-pharyngeal; pneumogastric, or par vagum; and spinal accessory. Three mixed nerves, with quite extensive distributions.

Ninth Pair.—Sublingual, or hypoglossal; a motor nerve distributed to the tongue.

Physiological Classification of the Cranial Nerves.

(a) *Nerves of Special Sense.*

Olfactory.

Optic.

Auditory.

Gustatory, comprising a part of the glosso-pharyngeal and a small filament from the facial to the lingual branch of the fifth.

(b) *Nerves of Motion.*

Nerves of motion of the eyeball, comprising the motor oculi communis, the patheticus, and the motor oculi externus.

Nerve of mastication, or motor root of the fifth.

Facial, sometimes called the nerve of expression.

Spinal accessory.

Sublingual.

(c) *Nerves of General Sensibility.*

Trifacial, or large root of the fifth.

A portion of the glosso-pharyngeal.

Pneumogastric.

In the above arrangement, the nerves are classified according to their properties at their roots. In their course, some of these nerves become mixed and their branches are both motor and sensory, such as the pneumogastric and the inferior maxillary branch of the trifacial.

The nerves of special sense are but slightly if at all endowed with general sensibility; and, with the exception of the gustatory nerves, they do not present a ganglion on their roots, in this, also, differing from the ordinary sensory nerves. They are capable, therefore, of conveying to the nerve-centres only certain peculiar impressions; such as odors, for the olfactory nerves; light, for the optic nerves; and sound, for the auditory nerves. The proper transmission of these impressions, however, involves the action of accessory organs, more or less complex; and we shall pass over the properties of these nerves until we come to treat in full of the special senses.

Motor Oculi Communis (Third Nerve).

The third cranial nerve is the most important of the motor nerves distributed to the muscles of the eyeball. Its physiology is readily understood in connection with its distribution, the only point at all obscure being its relations to the movements of the iris, upon which the results of experiments are somewhat contradictory. As an introduction to the study of the functions of this nerve, it will be necessary to describe its anatomical relations.

Physiological Anatomy.—Like all of the cranial nerves, this has an apparent origin, where it separates from the encephalon, and a deep origin, which is the last point to which its fibres can be traced in the substance of the brain; but the origin has not the physiological importance attached to its ultimate distribution.

The apparent origin of the third nerve is from the inner edge of the crus cerebri, directly in front of the pons Varolii, midway between the pons and the corpora albicantia. It presents here from eight to ten filaments, of nearly equal size, which soon unite into a single, rounded trunk.

The deep origin of the nerve has been studied by dissections of the encephalon fresh and hardened by different liquids. From the groove by which they emerge from the encephalon, the fibres spread out in a fan-shape, the middle filaments passing inward, the anterior, inward and forward, and the posterior, inward and backward. It is probable that the middle filaments pass to the median line and decussate with corresponding fibres from the opposite side. The anterior filaments pass forward and are lost in the optic thalamus. The posterior filaments on either side pass backward and decussate beneath the aqueduct of Sylvius. This apparent decussation of the fibres of origin of the third nerves is important in connection with the harmony of action of the muscles of the eyes and the iris upon the two sides.

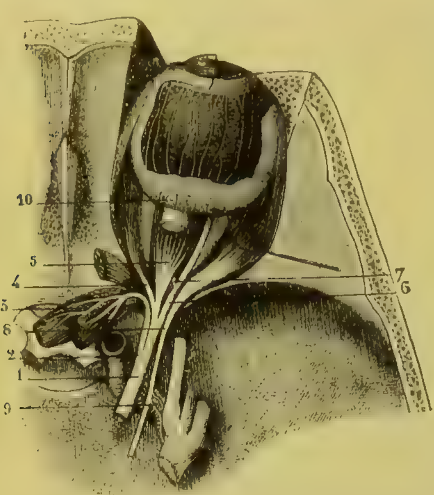


FIG. 196.—*Distribution of the motor oculi communis.* (Hirschfeld.)

1, *trunk of the motor oculi communis*; 2, *superior branch*; 3, *filaments which this branch sends to the superior rectus and the levator palpebri superioris*; 4, *branch to the internal rectus*; 5, *branch to the inferior rectus*; 6, *branch to the inferior oblique muscle*; 7, *branch to the lenticular ganglion*; 8, motor oculi externus; 9, filaments of the motor oculi externus anastomosing with the sympathetic; 10, *ciliary nerves*.

The distribution of the third nerve is very simple. As it passes into the orbit by the sphenoidal fissure, it divides into two branches. The superior, which is the smaller, passes to the superior rectus muscle of the eye, and certain of its filaments are continued to the levator palpebræ superioris. The inferior division breaks up into three branches. The internal branch passes to the internal rectus muscle; the inferior branch, to the inferior rectus; the external branch, the largest of the three, is distributed to the inferior oblique muscle, and, in its course, it sends a short and thick filament to the lenticular, or ophthalmic ganglion of the sympathetic. It is this branch which is supposed, through the short ciliary nerves passing from the lenticular ganglion, to furnish the motor influence to the iris. In its course, this nerve receives a few very delicate filaments from the cavernous plexus of the sympathetic and a branch from the ophthalmic division of the trifacial.

Properties and Functions of the Motor Oculi Communis.—Irritation applied to the root of the third nerve in a living animal produces contraction of the muscles to which it is distributed, but no pain. If the irritation, however, be applied a little farther on, in the course of the nerve, there are evidences of sensibility, which is readily explained by its communications with the ophthalmic branch of the trifacial. At its root, therefore, this nerve is exclusively motor, and its functions are connected entirely with the action of muscles.

Most of the important facts bearing upon the functions of the motor oculi are clearly demonstrable by dividing the nerve in a living animal and are illustrated by cases of its paralysis in the human subject. All physiologists who have divided the nerve in living animals are agreed with regard to the phenomena following its section, which depend upon paralysis of the voluntary muscles. These phenomena are as follows:

1. Falling of the upper eyelid, or blepharoptosis.

2. External strabismus, immobility of the eye (except in an outward direction), inability to rotate the eye on its antero-posterior axis in certain directions, with slight protrusion of the eye-ball.

3. Dilatation of the pupil, with a certain amount of interference with the movements of the iris.

The falling of the upper eyelid is constantly observed after division of the third nerve in living animals and always follows its complete paralysis in the human subject. An animal in which the nerve has been divided cannot raise the lid, but can approximate the lids more closely, by a voluntary effort. In the human subject, the falling of the lid gives to the face a very peculiar and characteristic expression. The complete loss of power shows that the levator palpebræ superioris muscle depends upon the third nerve entirely for its motor filaments. In pathology, external strabismus is very frequently observed without falling of the lid, the filament distributed to the levator muscle not being affected.

The external strabismus and the immobility of the eyeball except in an outward direction are due to paralysis of the internal, superior, and inferior recti muscles, the external rectus acting without its antagonist. This condition requires no farther explanation. These points are well illustrated by the experiment of dividing the nerve in rabbits. If the head of the animal be turned inward, exposing the eye to a bright light, the globe will turn outward, by the action of the external rectus; but, if the head be turned outward, the globe remains motionless.

It is somewhat difficult to note the effects of paralysis of the inferior oblique muscle, which is also supplied by the third nerve. This muscle, acting from its origin at the inferior and internal part of the circumference of the base of the orbit to its attachment at the inferior and external part of the posterior hemisphere of the eyeball, gives to the globe a movement of rotation on an oblique, horizontal axis, downward and backward, directing the pupil upward and outward. When this muscle is paralyzed, the superior oblique, having no antagonist, rotates the globe upward and inward, directing the pupil downward and outward. The action of the oblique muscles is observed when we move the head alternately toward one shoulder and the other. In the human subject, when the inferior oblique muscle on one side is paralyzed, the eye cannot move in a direction opposite to the movements of the head, as it does upon the sound side, so as to keep the pupil fixed, and the patient has double vision.

When all the muscles of the eyeball, except the external rectus and superior oblique, are paralyzed, as they are by section of the third nerve, the globe is slightly protruded, simply by the relaxation of most of its muscles. An opposite action is easily observed in a cat with the facial nerve divided, so that it cannot close the lids. When the cornea is touched, all of the muscles, particularly the four recti, act to draw the globe into the orbit, which allows the lid to fall slightly, and projects the little membrane which serves as a third eyelid in these animals.

Observations with regard to the influence of the third nerve upon the movements of the iris have not been so satisfactory in their results as those relating to the muscles of the eyeball. It will be remembered that this nerve sends a filament to the ophthalmic ganglion of the sympathetic, and that, from this ganglion, the short ciliary nerves take their origin and pass to the iris. The ganglia of the sympathetic system receive branches both from motor and sensory nerves belonging to the cerebro-spinal system, and the ophthalmic ganglion is no exception to this rule. While it is undoubtedly true that division of the third nerve affects the movements of the iris, it becomes a question whether this be a direct influence, or an influence exerted primarily upon the ganglion, not, perhaps, differing from the general effects upon the sympathetic ganglia that follow destruction of their branches of communication with the motor nerves.

The most important experimental observations with regard to the influence of the third nerve upon the iris are the following: Herbert Mayo made experiments on thirty pigeons, living or just killed, upon the action of the optic, the third, and the fifth nerves on the iris. He states that, when the third nerves are divided in the cranial cavity in a living pigeon, the pupils become fully dilated and do not contract on the admission of intense light; and, when the same nerves are pinched in the living or dead bird, the pupils are contracted for an instant on each stimulation of the nerves. The same results follow division or irritation of the optic nerves under similar conditions; but, when the third nerves have been divided, no change in the pupil ensues upon irritating the entire or divided optic nerves.

The above experiments are accepted by nearly all physiological writers; and the assumption is that the third nerves animate the muscular fibres that contract the pupil, the contraction produced by irritation of the optic nerves being reflex in its character. Later observers, however, have carried their experiments somewhat farther. Longet divided the motor oculi and the optic nerve upon the right side. He found that irritation of the central end of the divided optic nerve produced no movement of the pupil of the side upon which the motor oculi had been divided, but caused contraction of the iris upon the opposite side. This, taken in connection with the fact that, in amaurosis affecting one eye, the iris upon the affected side will not contract under the stimulus of light applied to the same eye, but will act when the uninjured eye is exposed to the light, farther illustrates the reflex action which takes place through these nerves.

The reflex action by which the iris is contracted is not instantaneous, like most of the analogous phenomena observed in the cerebro-spinal system, and its operations are rather characteristic of the sympathetic system and the non-striated muscular tissue. It has been found, also, by Bernard, in experiments upon rabbits, that the pupil is not immediately dilated after division of the third nerve. The method employed by Bernard, introducing a hook into the middle temporal fossa through the orbit and tearing the nerve, can hardly be accomplished without touching the ophthalmic branch of the fifth, which produces intense pain and is always followed by a more or less persistent contraction of the pupil. Several hours after the operation, however, the pupil is generally found dilated, and it may slowly contract when the eye is exposed to the light. In one experiment, this occurred after the eye had been exposed for an hour. But farther experiments by Bernard show that, although the pupil contracts feebly and slowly under the stimulus of light after division of the motor oculi, it will dilate under the influence of belladonna and can be made to contract by operating upon other nerves. It is well known, for example, that division or irritation of the fifth nerve produces contraction of the pupil. This takes place after as well as before division of the third nerve. Section of the sympathetic in the cervical region also contracts the pupil, and this occurs after paralysis of the motor oculi. These facts show that the third nerve is not the only one capable of acting upon the iris, and that it is not the sole avenue for the transmission of reflex influences.

Bernard also found that galvanization of the motor oculi itself did not produce contraction of the pupil, but this result followed when he galvanized the ciliary nerves coming from the ophthalmic ganglion. Chauveau states that, in experiments upon horses, he has not observed contraction of the pupil following galvanization of the motor oculi, although he has sometimes seen it in rabbits. At all events, contraction is by no means constant; and, when it occurs, it probably depends upon stimulation of the ciliary nerves themselves or irritation of the ophthalmic branch of the fifth, and not upon stimulation of the trunks of the third pair.

The movements of the iris will be treated of again, in connection with the physiology of vision; but we may here allude to an interesting fact observed by Müller, which relates to the action of the motores oculorum. When the eye is turned inward by a voluntary effort, the pupil is always contracted; and when the axes of the two eyes are made to converge strongly, as in looking at near objects, the contraction is very great.

The following case, kindly sent for examination by Dr. Althof, of the New York Eye Infirmary, illustrates, in the human subject, nearly all of the phenomena following paralysis of the motor oculi communis in experiments upon the lower animals:

The patient was a girl, nineteen years of age, with complete paralysis of the nerve upon the left side. There was slight protrusion of the eyeball, complete ptosis, with the pupil moderately dilated and insensible to ordinary impressions of light. The sight was not affected, but there was double vision, except when objects were placed before the eyes so that the axes were parallel, or when an object was seen with but one eye. The axis of the left eye was turned outward, but it was not possible to detect any deviation upward or downward. Upon causing the patient to incline the head alternately to one shoulder and the other, it was evident that the affected eye did not rotate in the orbit but moved with the head. This seemed to be a case of complete and uncomplicated paralysis of the third nerve.

Patheticus, or Trochlearis (Fourth Nerve).

Except as regards the influence of the motor oculi communis upon the iris, the patheticus is to be classed with the other motor nerves of the eyeball. Its physiology is extremely simple and resolves itself into the action of a single muscle, the superior oblique. It will be necessary, therefore, only to describe its origin, distribution, and connections.

Physiological Anatomy.—The apparent origin of the patheticus is from the superior peduncles of the cerebellum; but it may be easily traced to the valve of Vieussens. The deep roots, which are covered by an extremely thin layer of nerve-substance, can be traced, passing from without inward, to the following parts: One filament is lost in the substance of the peduncles; other filaments pass from before backward into the valve of Vieussens and are lost, and a few pass into the frenulum; a few filaments pass backward and are lost in the corpora quadrigemina; but the greatest number pass to the median line and decussate with corresponding filaments from the opposite side. The decussation of the fibres of origin of the fourth nerves has the same physiological significance as the decussation of the roots of the third. From this origin, the patheticus passes into the orbit by the sphenoidal fissure and is distributed to the superior oblique muscle of the eyeball. In the cavernous sinus, it receives branches of communication from the ophthalmic branch of the fifth, but these are not closely united with the nerve. A small branch passes into the tentorium, and one joins the lachrymal nerve, these, however, being exclusively sensitive and coming from the ophthalmic branch of the fifth. It also receives a few filaments from the sympathetic.

Properties and Functions of the Patheticus.—Direct observations upon the patheticus in living animals have shown that it is motor, and its galvanization excites contraction of the superior oblique muscle only. The question of the function of the nerve, therefore, resolves itself simply into the mode of action of the superior oblique muscle. This muscle arises just above the inner margin of the optic foramen, passes forward, along the upper wall of the orbit at its inner angle, to a little cartilaginous ring which serves as a pulley. From its origin to this point it is muscular. Its tendon becomes rounded just before it passes through the pulley, where it makes a sharp curve, passes outward and slightly backward, and becomes spread out to be attached to the globe at the superior and external part of its posterior hemisphere. It acts upon the eyeball from the pulley at the upper and inner portion of the orbit as the fixed point and rotates the eye upon an oblique, horizontal axis, from below upward, from without inward, and from behind forward. By its action, the pupil is directed downward and outward. It is the direct antagonist of the inferior oblique, the action of which has been described in connection with the motor oculi communis. When the patheticus is paralyzed, the eyeball is immovable, as far as rotation is concerned; and, when the head is moved toward the shoulder, the eye does not rotate to maintain the globe in the same relative position, and we have double vision.

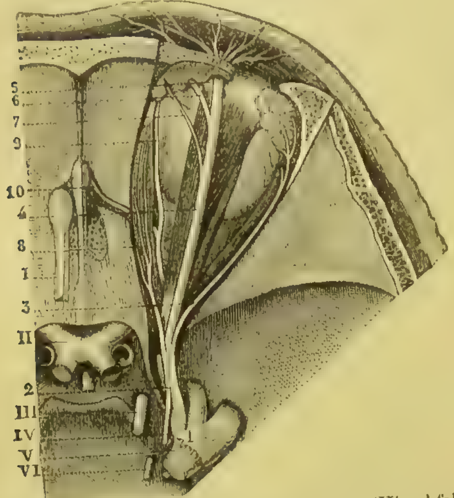


FIG. 197.—*Distribution of the patheticus.* (Hirschfeld.)
I, olfactory nerve; II, optic nerves; III, motor oculi communis; IV, *patheticus, by the side of the ophthalmic branch of the fifth, and passing to the superior oblique muscle;* VI, motor oculi externus; 1, ganglion of Gasser; 2, 3, 4, 5, 6, 7, 8, 9, 10, ophthalmic division of the fifth nerve, with its branches.

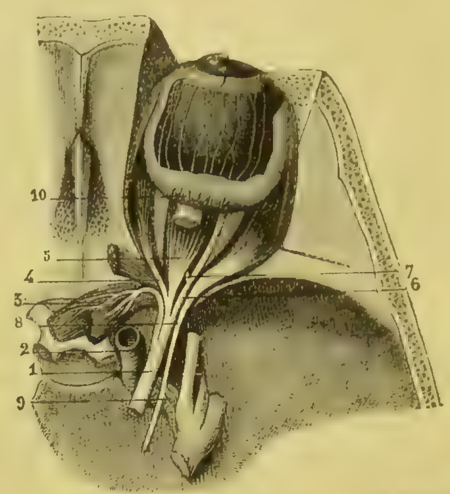


FIG. 198.—*Distribution of the motor oculi externus.* (Hirschfeld.)
1, trunk of the motor oculi communis, with its branches (2, 3, 4, 5, 6, 7); 8, *motor oculi externus, passing to the external rectus muscle;* 9, *filaments of the motor oculi externus anastomosing with the sympathetic;* 10, ciliary nerves.

Motor Oculi Externus, or Abducens (Sixth Nerve).

Like the patheticus, the motor oculi externus is distributed to but a single muscle, the external rectus. Its uses, therefore, are apparent from a study of its distribution and properties.

Physiological Anatomy.—The apparent origin of the sixth nerve is from the groove which separates the anterior corpus pyramidale of the medulla oblongata from the pons Varolii, and from the upper portion of the medulla and the lower portion of the pons next the groove. Its origin at this point is by two roots: an inferior, which is the larger, and comes from the corpus pyramidale; and a superior root, sometimes wanting, which seems to come from the lower portion of the pons. All anatomists are agreed that the deep fibres of origin of this nerve pass to the gray matter in the floor of the fourth ventricle. Vulpian has followed these fibres to within about two-fifths of an inch of the median line, but they could not be traced beyond this point. It is not known that the fibres of the two sides decussate. From this origin, the nerve passes into the orbit by the sphenoidal fissure and is distributed exclusively to the external rectus muscle of the eyeball. In the cavernous sinus, it anastomoses with the sympathetic through the carotid plexus and Meckel's ganglion. It also receives sensitive filaments from the ophthalmic branch of the fifth. It is stated by some anatomists that this nerve occasionally sends a small filament to the ophthalmic ganglion; and it is supposed by Longet that this branch, which is exceptional, exists in those cases in which paralysis of the motor oculi communis, which usually furnishes all the motor filaments to this ganglion, is not attended with immobility of the iris.

Properties and Functions of the Motor Oculi Externus.—Direct experiments have shown that the motor oculi externus is entirely insensible at its origin, its stimulation producing contraction of the external rectus muscle and no pain. The same experiments illustrate the function of the nerve, inasmuch as its irritation is followed by powerful contraction of the muscle and deviation of the eye outward. Division of the nerve in the lower animals or its paralysis in the human subject is attended with internal, or converging strabismus, due to the unopposed action of the internal rectus muscle.

With regard to the associated movements of the eyeball, it is a curious fact that all of the muscles of the eye that have a tendency to direct the pupil inward or to produce the simple movements upward and downward, viz., the internal, inferior, and superior recti, are animated by a single nerve, the motor oculi communis, this nerve also supplying the inferior oblique; and that each muscle that has a tendency to move the globe so as to direct the pupil outward, except the inferior oblique, viz., the superior oblique and the external rectus, is supplied by a special nerve. The various movements of the eyeball will be studied more minutely in connection with the physiology of vision.

Motor Nerves of the Face.

The motor nerves of the face are, the small, or motor root of the fifth, and the portio dura of the seventh, or the facial. The first of these nerves is distributed to the deep muscles, those concerned in the act of mastication; and the second, the facial, supplies the superficial muscles of the face and is sometimes called the nerve of expression. These nerves are not so simple in their anatomy and physiology as the motor nerves of the eyeball. The nerve of mastication, at its origin, is deeply situated at the base of the brain and is exposed and operated upon with difficulty. It passes out of the cranium, closely united with one of the great sensitive branches of the fifth, and its distribution has been most successfully studied by experiments in which it is divided in the cranial cavity. The origin of the facial is also reached with great difficulty. It communicates with other nerves, and its physiology has been most satisfactorily studied by dividing it at its origin or in different portions of its course. In treating of these nerves, we shall first, as in the case of the motor nerves of the eye, study their properties at their roots, noting the phenomena following their galvanization and section. It will be necessary, also, to describe their origin and distribution, as far as has been ascertained by dissection.

Nerve of Mastication (the Small, or Motor Root of the Fifth Nerve).

The motor root of the fifth nerve is entirely distinct from its sensitive portion, until it emerges from the cranial cavity by the foramen ovale. It is then closely united with the inferior maxillary branch of the large root; but at its origin it has been shown to be motor, and its section in the cranial cavity has demonstrated its distribution to a particular set of muscles.

Physiological Anatomy of the Nerve of Mastication.—The apparent origin of the fifth nerve is from the lateral portion of the pons Varolii. The small, or motor root arises from a point a little higher and nearer the median line than the large root, from which it is separated by a few fibres of the white substance of the pons. At the point of apparent origin, the small root presents from six to eight rounded filaments. If a thin layer of the pons covering these filaments be removed, the roots will be found penetrating its substance, becoming flattened, passing under the superior peduncles of the cerebellum, and going to the anterior wall of the fourth ventricle. At this point, they change their direction, passing now from without inward and from behind forward toward the median line, the fibres diverging rapidly. The posterior fibres pass to the median line, and certain of them decussate with the fibres from the opposite side. The anterior fibres pass toward the aqueduct of Sylvius and are lost. The fibres become changed in their character when they are followed inward beyond the anterior wall of the fourth ventricle. Here they lose their white color, become gray, and present numerous globules of gray substance between their filaments.

From the origin above described, the small root passes beneath the ganglion of Gasser—from which it sometimes, though not constantly, receives a filament of communication—lies behind the inferior maxillary branch of the large root, and passes out of the cranial cavity by the foramen ovale. Within the cranium, the two roots are distinct; but, after the small root passes through the foramen, it is united by a mutual interlacement of fibres with the sensitive branch.

The course of the motor root of the fifth possesses little physiological interest. It is sufficient in this connection to note that the inferior maxillary nerve, made up of the motor root and the inferior maxillary branch of the sensitive root, just after it passes out

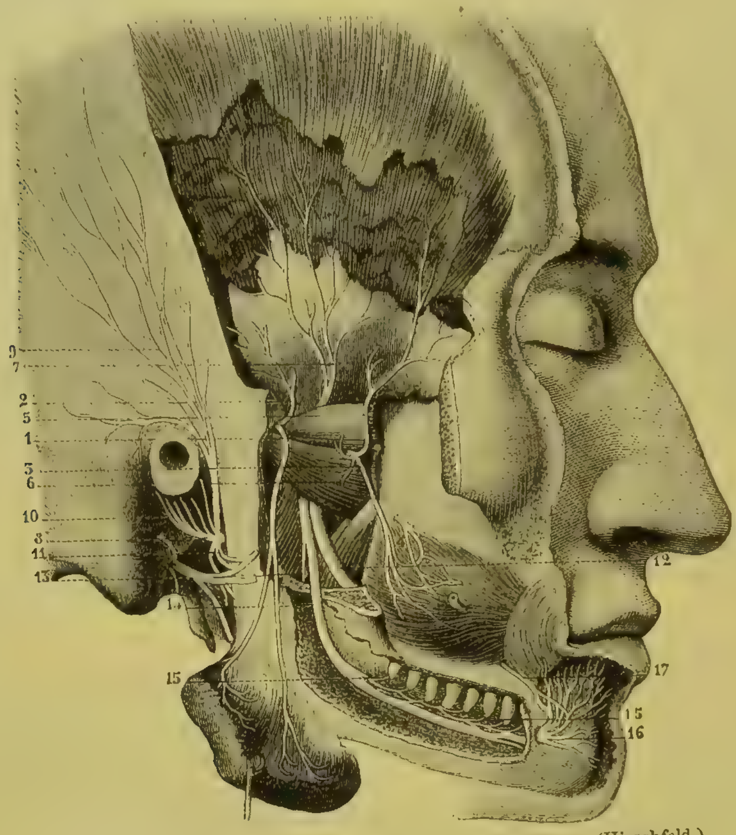


FIG. 199.—*Distribution of the small root of the fifth nerve.* (Hirschfeld.)
1, *branch to the masseter muscle*; 2, *filament of this branch to the temporal muscle*; 3, *buccal branch*; 4, *branches anastomosing with the facial nerve*; 5, *filament from the buccal branch to the temporal muscle*; 6, *branches to the external pterygoid muscle*; 7, *middle deep temporal branch*; 8, auriculo-temporal nerve; 9, temporal branches; 10, auricular branches; 11, anastomosis with the facial nerve; 12, lingual branch; 13, *branch of the small root to the mylo-hyoid muscle*; 14, inferior dental nerve, with its branches (15, 15); 16, mental branch; 17, anastomosis of this branch with the facial nerve.

by the foramen ovale, divides into two branches, anterior and posterior. The anterior branch, which is the smaller, is composed almost entirely of motor filaments and is distributed to the muscles of mastication. It gives off five branches. The first of these passes to be distributed to the masseter muscle, in its course occasionally giving off a small branch to the temporal muscle and a filament to the articulation of the inferior maxilla with the temporal bone. The two deep temporal branches are distributed to the temporal muscle. The buccal branch sends filaments to the external pterygoid and to the temporal muscle, and a small branch is distributed to the internal pterygoid muscle. From the posterior branch, which is chiefly sensitive but contains some motor filaments, branches are sent to the mylo-hyoid muscle and to the anterior belly of the digastric. In addition, the motor branch of the fifth sends filaments to the tensor muscles of the velum palati.

The above description shows, in general terms, the distribution of the nerve of mastication, without taking into consideration its various anastomoses, the most important of which are with the facial. Physiological experiments have shown that the buccinator muscle receives no motor filaments from the fifth but is supplied entirely by the facial. The buccal branch of the fifth sends motor filaments only, to the external pterygoid and the temporal, its final branches of distribution being sensitive and going to integument and to mucous membrane.

In treating of the function of digestion, we have given a table of the muscles of mastication, with a description of their action. It will be seen by reference to this table that the following muscles depress the lower jaw; viz., the anterior belly of the digastric, the mylo-hyoid, the genio-hyoid, and the platysma myoides. Of these, the digastric and the mylo-hyoid are animated by the motor root of the fifth; the genio-hyoid is supplied by filaments from the sublingual; and the platysma myoides, by branches from the facial and from the cervical plexus. All of the muscles which elevate the lower jaw and move it laterally and antero-posteriorly, viz., the temporal, masseter, and the internal and external pterygoids (the muscles most actively concerned in mastication) are animated by the motor root of the fifth.

Properties and Functions of the Nerve of Mastication.—The anatomical distribution of the small root of the fifth nerve points at once to its function. Charles Bell, whose ideas of the nerves were derived almost entirely from their anatomy, called it the nerve of mastication, in 1821, although he does not state that any experiments were made with regard to its function. All anatomical and physiological writers since that time have adopted this view. It would be difficult, if not impossible, to galvanize the root in the cranial cavity in a living animal; but its galvanization in animals just killed determines very marked movements of the lower jaw. Experiments have clearly demonstrated the physiological properties of the small root, which is without doubt solely a nerve of motion.

The observations upon the division of the fifth pair in the cranial cavity are most interesting in connection with the functions of its sensitive branches, and will be referred to in detail in treating of the properties of the large root. In addition to the loss of sensibility following section of the entire nerve, Bernard has carefully noted the effects of division of the small root, which cannot be avoided in the operation. In rabbits, the paralysis of the muscles of mastication upon one side, and the consequent action of the muscles upon the unaffected side only, produce, a few days after the operation, a remarkable change in the appearance of the incisor teeth. As the teeth in these animals are gradually worn away in mastication and reproduced, the lower jaw being deviated by the action of the muscles of the sound side, the upper incisor of one side and the lower incisor of the other touch each other but slightly and the teeth are worn unevenly. This makes the line of contact between the four incisors, when the jaws are closed, oblique instead of horizontal. We have often divided the fifth pair in the cranial cavity in rabbits, by the method employed by Magendie and Bernard, and have repeatedly verified these observations.

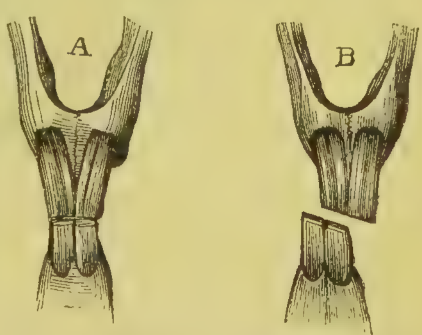


FIG. 200.—*Incisors of the rabbit, before and after section of the nerve of mastication.* (Bernard.)

A, incisors, normal condition.
B, incisors, seven days after section of the nerve on one side.

There is little left to say with regard to the functions of the motor root of the fifth nerve, in addition to our description of the action of the muscles of mastication, contained in the chapters on digestion, except as regards the action of the filaments sent to the muscles of the velum palati. In deglutition, the muscles of mastication are indirectly involved. This act cannot be well performed unless the mouth be closed by these muscles. When the food is brought in contact with the velum palati, muscles are brought into action which render this membrane tense, so that the opening is adapted to the size of the alimentary bolus. These muscles are animated by the motor root of the fifth. This nerve, then, is not only the nerve of mastication, animating all of the muscles concerned in this act, except two of the most unimportant depressors of the lower jaw (the genio-hyoid and the platysma myoides), but it is concerned indirectly in deglutition.

Facial Nerve, or Nerve of Expression (the Portio Dura of the Seventh Nerve).

The facial, the portio dura of the seventh according to the arrangement of Willis, is one of the most interesting of the cranial nerves. Its anatomical relations are quite intricate, and its communications with other nerves, very numerous. As far as can be determined by experiments upon living animals, this nerve is exclusively motor at its origin; but in its course it presents anastomoses with the sympathetic, with branches of the fifth, and with the cervical nerves, undoubtedly receiving sensory filaments. While the chief physiological interest attached to this nerve depends upon its action upon muscles, it is important to study its origin, distribution, and communications.

Physiological Anatomy of the Facial Nerve.—The portio dura of the seventh has its apparent origin from the lateral portion of the medulla oblongata, in the groove between the olivary and the restiform body, just below the border of the pons Varolii, its trunk being internal to the trunk of the portio mollis, or auditory nerve. It is separated from the auditory by the two filaments constituting what is known as the intermediary nerve of Wrisberg, or the portio inter duram et mollem. As this little nerve joins the facial, it must be included in its root.

There are certain pathological considerations which render the deep, or real origin of the facial a question of the greatest interest and importance. In hemiplegia due to injury of the substance of the encephalon, particularly from hæmorrhage, there is almost always more or less paralysis of the superficial muscles of the face. It has been observed that, in certain cases, the facial paralysis exists upon the same side as the hemiplegia (the side opposite to the cerebral lesion), while in others, the palsy of the face is upon the same side as the lesion, the general hemiplegia being, as usual, upon the opposite side. To explain these phenomena theoretically, we must assume that, in some cases, the brain-lesion is to be located at a point where it involves the filaments of origin of the facial (following them from without inward) before they decussate, which would produce facial paralysis upon the same side as the lesion and none upon the side affected with general hemiplegia; while, in other cases, the injury to the brain involves the roots of the facial after they have decussated, when the paralysis of the face would be upon the same side as the paralysis of the rest of the body. It would be interesting to see how far these pathological facts, with their theoretical explanation, correspond with anatomical researches into the real origin of the nerves.

Many anatomists have endeavored to trace the fibres of the facial from their point of emergence from the encephalon to their true origin, but with results not entirely satisfactory. At the present day, it is pretty generally agreed that the fibres pass inward, with one or two deviations from a straight course, to the floor of the fourth ventricle, where they spread out and become fan-shaped. In the floor of the fourth ventricle, certain of the fibres have been thought to terminate in the cells of the gray substance, and others have been traced to the median line, where they decussate; the course of most of the fibres, however, has never been satisfactorily established.

It is evident, from physiological experiments, that the decussation of the fibres in the floor of the fourth ventricle itself is not very important. Vulpian has made, in dogs and rabbits, a longitudinal section in the middle line of the ventricle, which would necessarily have divided the fibres passing from one side to the other, without producing notable paralysis of the facial nerves upon either side. This single fact is sufficient to show that the main decussation of the fibres animating the muscles of the face takes place, if at all, at some other point.

The pathological facts bearing upon the question of decussation of the filaments of origin of the facial have long been recognized. They are, in brief, as follows: When there is a lesion of the brain-substance anterior to the pons Varolii, the phenomena due to paralysis of the facial are observed upon the same side as the hemiplegia, opposite the side of injury to the brain. When the lesion is either in the pons or below it, the face is

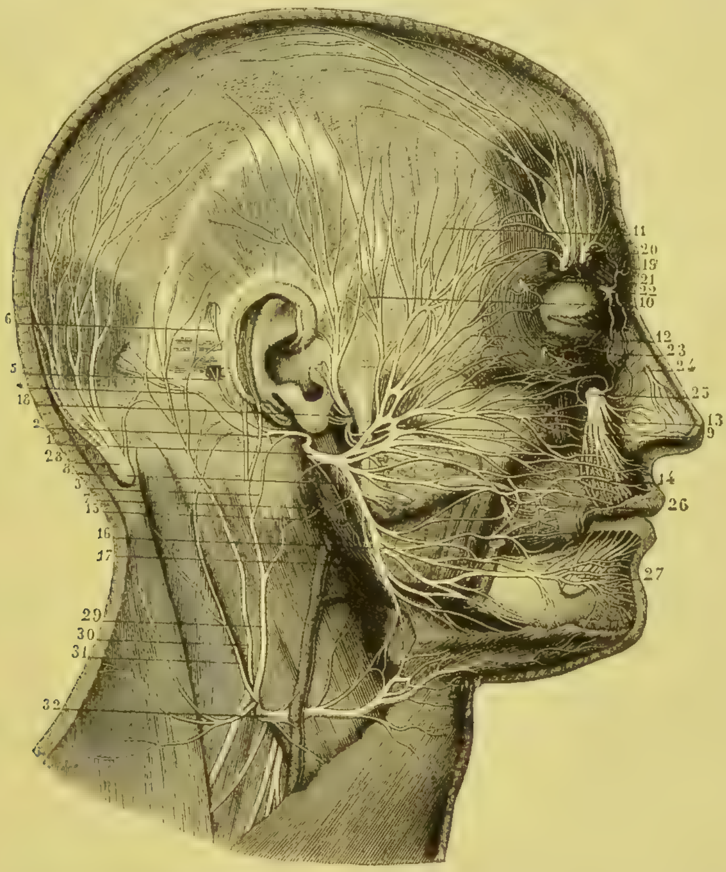


Fig. 201.—*Superficial branches of the facial and the fifth.* (Hirschfeld.)
1, *trunk of the facial;* 2, *posterior auricular nerve;* 3, *branch which it receives from the cervical plexus;* 4, *occipital branch;* 5, 6, *branches to the muscles of the ear;* 7, *digastric branches;* 8, *branch to the stylo-hyoid muscle;* 9, *superior terminal branch;* 10, *temporal branches;* 11, *frontal branches;* 12, *branches to the orbicularis palpebrarum;* 13, *nasal, or suborbital branches;* 14, *buccal branches;* 15, *inferior terminal branch;* 16, *mental branches;* 17, *cervical branches;* 18, superficial temporal nerve (branch of the fifth); 19, 20, frontal nerves (branches of the fifth); 21, 22, 23, 24, 25, 26, 27, branches of the fifth; 28, 29, 30, 31, 32, branches of the cervical nerves.

affected upon the same side, and not upon the side of the hemiplegia. In view of these facts, the remarkable phenomenon of hemiplegia upon one side and facial paralysis upon the other is regarded as indicating, with tolerable certainty, that the injury to the brain has occurred upon the same side as the facial paralysis, either within or posterior to the pons Varolii. It is unnecessary to enter into a farther discussion of these facts, which are accepted by nearly all writers upon diseases of the nervous system and may be regarded as settled; and the only question is, how far they can be explained by the anatomy of the parts.

As we have just seen, the fibres of origin of the facial have been traced to the floor of the fourth ventricle, where a few decussate, but the rest are lost. The question now is, whether or not the fibres pass up through the pons and decussate above, as the pathological facts just noted would seem to indicate. Anatomical researches upon this point are entirely unsatisfactory; and the existence of such a decussation has never been clearly demonstrated. The pathological observations, nevertheless, remain; and, however indefinite anatomical researches may have been, there can be no doubt that lesions in one-half of the pons affect the facial upon the same side, while lesions above have a crossed action. The most that we can say upon this point is, that it is a reasonable inference from pathological facts that the nerves decussate anterior to the pons.

It will be only necessary to describe in a general way the course of the fibres of distribution of the facial. The main root of the facial, the auditory nerve, and the delicate intermediary nerve of Wrisberg pass together into the internal auditory meatus. At the bottom of the meatus, the facial and the nerve of Wrisberg enter the aquæductus Fallopii, following its course through the petrous portion of the temporal bone. In the aqueduct, the nerve of Wrisberg presents a little gangliform enlargement, of a reddish color, which has been shown to contain nerve-cells. The main root and the intermediary nerve then unite and form the common trunk of the facial, which emerges from the cranial cavity by the stylo-mastoid foramen.

In the aquæductus Fallopii, the facial gives off numerous branches, as follows:

1. The large petrosal branch is given off at the gangliform enlargement and goes to Meckel's ganglion.

2. The small petrosal branch is given off at the gangliform enlargement or a very short distance beyond it, and passes to the otic ganglion.

3. A small branch, the tympanic, is distributed to the stapedius muscle.

4. The chorda tympani, a branch of great physiological interest, passes through the cavity of the tympanum and joins the lingual branch of the inferior maxillary division of the fifth as it passes between the two pterygoid muscles, with which nerve it becomes closely united.

5. Opposite to the point of origin of the chorda tympani, a communicating branch passes between the facial and the pneumogastric, connecting these nerves by a double inosculation.

The five branches above described are given of in the aquæductus Fallopii. The following branches are given off after the nerve has emerged from the cranial cavity:

1. Just after the facial has passed out at the stylo-mastoid foramen, it sends a small communicating branch to the glosso-pharyngeal nerve. According to Sappey, this branch is sometimes wanting.

2. The posterior auricular nerve is given off by the facial a little below the stylo-mastoid foramen. Its superior branch is distributed to the retrahens aurem and the attollens aurem. In its course, this nerve receives a communicating branch of considerable size from the cervical plexus, by the auricularis magnus. It sends some filaments to the integument. The inferior, or occipital branch, the larger of the two, is distributed to the occipital portion of the occipito-frontalis muscle and to the integument.

3. The digastric branch is given off near the root of the posterior auricular. It is distributed to the posterior belly of the digastric muscle. In its course, it anastomoses with filaments from the glosso-pharyngeal nerve. From the plexus formed by this anastomosis, filaments are given off to the digastric and to the stylo-hyoid muscle.

4. Near the stylo-mastoid foramen, a small branch is given off, which is distributed exclusively to the stylo-hyoid muscle.

5. Near the stylo-mastoid foramen, or sometimes a little above it, a long and exceed-

ingly delicate branch is given off, which is not noticed in most works on anatomy. It is described, however, by Hirschfeld, under the name of the lingual branch. It passes behind the stylo-pharyngeal muscle, and then by the sides of the pharynx to the base of the tongue. In its course, it receives one or two branches from the glosso-pharyngeal nerve, which are nearly as large as the original branch from the facial. As it passes to the base of the tongue, it anastomoses again by numerous filaments with the glosso-pharyngeal. It then sends filaments of distribution to the mucous membrane, and finally passes to the stylo-glossus and the palato-glossus muscle.

Having given off these branches, the trunk of the facial passes through the parotid gland, dividing into its two great terminal branches:

1. The temporo-facial branch, the larger, passes upward and forward to be distributed to the superficial muscles of the upper part of the face; viz., the attrahens aurem, the frontal portion of the occipito-frontalis, the obicularis palpebrarum, corrugator supercilii, pyramidalis nasi, levator labii superioris, levator labii superioris alæque nasi, the dilators and compressors of the nose, part of the buccinator, the levator anguli oris, and the zygomatic muscles. In its course, it receives branches of communication from the auriculo-temporal branch of the inferior maxillary nerve. It joins also with the temporal branch of the superior maxillary and with branches of the ophthalmic. In its course, it thus becomes a mixed nerve and is distributed in part to integument.

2. The cervico-facial nerve passes downward and forward to supply the buccinator, orbicularis oris, risorius, levator labii inferioris, depressor labii inferioris, depressor anguli oris, and platysma.

Summary of the Anastomoses and Distribution of the Facial.—In the aquæductus Fallopii, filaments of communication go to Meckel's ganglion and the otic ganglion of the sympathetic. The chorda tympani joins the lingual branch of the inferior maxillary division of the fifth. A branch is also sent to the pneumogastric. After the nerve has passed out by the stylo-mastoid foramen, it sends a communicating branch to the glosso-pharyngeal, and receives a branch from the auricularis magnus. It anastomoses, also, outside of the cranium, with the glosso-pharyngeal. In the course of the nerve, it receives anastomosing filaments from the three great divisions of the fifth.

It is thus seen that the facial, in its course, receives numerous filaments from the great sensitive nerve of the face. Certain of its fibres of distribution go to integument.

The muscles supplied by the facial are the stapedius, and probably the tensor tympani, of the internal ear, the muscles of the external ear, the occipito-frontalis, the posterior belly of the digastric, the stylo-hyoid, the stylo-glossus, and the palato-glossus. The two great branches of distribution, the temporo-facial and the cervico-facial, are distributed to all of the superficial muscles of the face, leaving the deep muscles, or the muscles of mastication, to be supplied by the motor root of the fifth. In addition, it supplies in part the platysma myoides.

Properties and Functions of the Facial Nerve.—It has long been recognized that the facial is the motor nerve of the superficial muscles of the face, and that its division produces paralysis of motion and no marked effects upon sensation. It is evident, also, from the numerous communications of the facial with the fifth, that it probably contains in its course sensitive fibres. Indeed, all who have operated upon this nerve have found that it is slightly sensitive after it has emerged from the cranial cavity. It is a question, however, of great importance to determine whether or not the facial be endowed with sensibility by virtue of its own fibres of origin. The main root is evidently from the motor tract, resembles the anterior roots of the spinal nerves, and is distributed to muscles; but this is joined by the intermediary nerve of Wrisberg, which presents a small enlargement, undoubtedly containing nerve-cells, somewhat analogous to the ganglia upon the posterior roots of the spinal nerves.

Direct observations upon the properties of the facial as it penetrates the auditory canal, and before it has received any anastomosing branches from sensitive nerves, must be to a certain extent unsatisfactory. All who have experimented upon the nerves know that the pain and depression which attend so serious an operation as that of exposing the roots of a nerve in the cranial cavity are sufficient to render it doubtful whether the parts be in a condition to exhibit a slight degree of sensibility, which the nerves may possess when perfectly normal. Magendie and Bernard, who have exposed the roots of origin of the facial, state unreservedly that they are absolutely insensible; but Longet very justly remarks that the conditions under which such observations are made have not been, in his hands, sufficiently favorable to admit of a rigorous conclusion upon this point. The testimony of direct experimentation is in favor of the insensibility of the facial at its origin. It is true that the intermediary nerve of Wrisberg has a certain anatomical resemblance to the sensitive nerves, chiefly by virtue of its gangliform enlargement; but direct experiments are wanting to show that it is actually sensitive. In view of this fact, it is impossible to reason conclusively from its anatomical characters alone.

The most convenient way to consider the functions of the facial will be to take up *seriatim* the properties and distribution of its different branches.

Functions of the Branches of the Facial within the Aqueduct of Fallopius.—The first branch, the large petrosal, is the motor root of Meckel's ganglion. This will be referred to again in connection with the sympathetic system. The second branch, the small petrosal, is one of the motor roots of the otic ganglion of the sympathetic. The third branch, the tympanic, is distributed exclusively to the stapedius muscle. The second and third branches will be again considered in connection with the physiology of the internal ear. The fourth branch, the chorda tympani, is so important that it demands special consideration. The fifth branch is given off opposite the origin of the chorda tympani and passes to the pneumogastric, to which nerve it probably supplies motor filaments. We have already seen, in studying the properties of the roots of the facial, that, in this branch, sensory filaments pass from the pneumogastric and constitute a part of the sensory connections of the facial.

Functions of the Chorda Tympani.—This branch passes between the bones of the ear and through the tympanic cavity to the lingual branch of the inferior maxillary division of the fifth, which it joins at an acute angle, between the pterygoid muscles. It has been a question whether this nerve be simply enclosed in the sheath of the lingual branch of the fifth or be so closely connected with it that it cannot be traced to a distinct distribution. Upon this point we are disposed to adopt the opinion of Sappey, who, as the result of minute dissections, regards the union as complete, "fibril to fibril." As regards the portion of the facial which furnishes the filaments of the chorda tympani, it is impossible to determine anatomically whether these come from the main root or from the intermediary nerve of Wrisberg, as the fibres of these roots are closely united before the chorda tympani is given off.

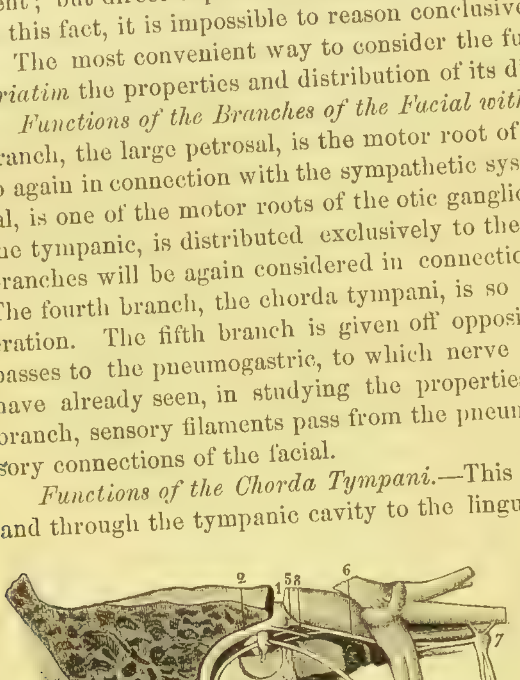


FIG. 202.—*Chorda-tympani nerve.* (Hirschfeld.)
1, 2, 3, 4, facial nerve passing through the aquæductus Fallopii; 5, gangliform enlargement; 6, great petrosal nerve; 7, spheno-palatine ganglion; 8, small petrosal nerve; 9, *chorda tympani*; 10, 11, 12, 13, various branches of the facial; 14, 14, 15, glosso-pharyngeal nerve.

The only questions that we propose to consider in this connection relate to the functions of the chorda tympani as a nerve of gustation, and as it influences the secretion of the submaxillary gland.

There can be no doubt with regard to the influence of the chorda tympani upon the sense of taste in the anterior portion of the tongue. Without citing all of the experiments and pathological observations bearing upon this question, it is sufficient to state that, in cases of disease or injury in which the root of the facial is involved so that the chorda tympani is paralyzed, in addition to the ordinary phenomena of paralysis of the superficial muscles of the face, there is loss of taste in the anterior portion of the tongue upon the side corresponding to the lesion. Numerous cases of this kind are quoted in works on physiology, which will be referred to more fully in connection with the subject of gustation.

In 1863, we had under observation, for several months, a soldier who received a gun-shot-wound, the ball passing through the head, entering just above the ala of the nose upon the left side and emerging behind the mastoid process of the right temporal bone. The wound was nearly healed while he was under observation, and the usual symptoms of complete facial paralysis were manifested upon the right side. The buccinator and the orbicularis oculi were completely paralyzed. Vision in the right eye was slightly impaired, but was improving. The hearing was perfect, and there were no abnormal phenomena except those apparently due to injury of the facial. The sense of taste was entirely abolished in the anterior portion of the tongue upon the right side. Experiments upon this point were repeatedly made with salt, pepper, and other sapid substances. This patient was exhibited in two successive years to the class at the Bellevue Hospital Medical College, when the above-mentioned facts were demonstrated.

Physiologists have observed loss of taste in the anterior portion of the tongue, in dogs, cats, and other animals, following section of the root of the facial or of the chorda tympani. Some observers, it is true, have failed to note the phenomena satisfactorily, and there is some difference of opinion with regard to the real origin of the gustatory filaments; but the fact that the chorda tympani influences the taste can hardly be doubted. Adopting this view, we shall defer the full consideration of the functions of the chorda tympani until we come to treat of the special sense of taste.

Schiff, in 1851, was the first to note the influence of the chorda tympani upon the secretion of the submaxillary gland. In his experiments, the chorda tympani was exposed and the flow of the submaxillary saliva noted. Upon division of the chorda tympani, the flow of saliva was momentarily increased, but was soon arrested; and subsequently, stimulation of the gustatory sense failed to induce secretion, as it does when the nerve is intact. Similar experiments, upon a much more extended scale, were made by Bernard, in the following way:

The duct of the submaxillary gland was exposed in a dog, and into it was fixed a silver canula. The nervous filaments going to the gland from the lingual branch of the fifth were then isolated. A little vinegar introduced into the mouth caused an abundant flow of saliva from the tube. The chorda tympani was then divided, by introducing a sharp instrument through the membrane into the tympanic cavity. After division of the nerve, the introduction of vinegar into the mouth failed to excite the salivary secretion. From this and similar experiments, Bernard concludes that the chorda tympani is the motor nerve of the submaxillary gland. After having arrested the secretion by section of the chorda tympani, the action of the gland was excited by galvanization of the peripheral end of the nerve. Section of the facial after its passage out of the stylo-mastoid foramen did not arrest the action of the parotid; but section of the nerve within the cranium arrested the secretion, both of the parotid and submaxillary.

These observations show conclusively that the facial, either through branches from its proper roots or its filaments of communication with other nerves, regulates the secretion of at least two of the salivary glands.

Influence of Various Branches of the Facial upon the Movements of the Palate and Uvula.—There can be little doubt that filaments from the facial animate certain of the movements of the velum palati and uvula. It has been observed that, in certain cases of facial paralysis, the palate upon one side is perfectly flaccid and the uvula is drawn to the opposite side; but these phenomena do not occur unless the nerve be affected at its root or within the aquæductus Fallopii. It is true that the uvula is frequently drawn to one side or the other in persons unaffected with facial paralysis, but it is none the less certain that it is deviated as a consequence of paralysis of the facial in some instances.

Direct experiments upon the roots of the facial have not been followed by uniform results. Debrou mentions one experiment in which galvanization of the facial within the cranial cavity produced decided contraction of the muscles of the palate; but, in four others, the results were negative. Nuhn, however, produced contractions of these muscles by galvanization of the nerve in the cranium in a man immediately after decapitation. The experiments of Bernard upon this point are the most conclusive; but while they show, beyond a doubt, that the facial animates the movements of the soft palate, they do not indicate the course of the filaments from the nerve to the muscles. In these experiments, made in connection with M. Davaine, the whole of the velum palati was exposed in a large-sized dog, by cutting through the hyoid bone. The trunk of the glosso-pharyngeal nerve was then exposed in the neck, near its point of emergence at the posterior foramen lacerum, and the animal was killed by section of the spinal cord just below the origin of the cranial nerves. This being done, the glosso-pharyngeal was galvanized, which produced violent contractions of the velum, the pillars of the fauces, and a part of the pharynx, upon one side. The nerve was then divided, and galvanization was applied to its peripheral end without producing any movement in the velum. The central end was then galvanized, when the contractions were as vigorous as when the nerve was intact. This result would lead to the supposition that contractions of the muscles of the palate following galvanization of the glosso-pharyngeal are reflex and not due to the direct action of filaments of distribution from this nerve. In a second experiment, the parts were exposed in the same way, and, in addition, the facial was divided upon the right side at its entrance into the internal auditory canal. The glosso-pharyngeal nerve was then galvanized upon the side on which the facial had been divided, with the effect of producing movements of the pillars of the fauces, but not of the velum palati itself. The glosso-pharyngeal was then galvanized upon the side on which the facial was intact, which produced movements of the velum the same as in the first experiment. Galvanization of the pneumogastric, the sublingual, and the lingual branch of the fifth, failed to produce movements of the velum.

"The first experiment proves that the glosso-pharyngeal nerve is not the motor nerve of the velum palati, but that it induces reflex movements by the excitation which it transmits to the nervous centre, an excitation which is carried to the parts by another nerve.

"The second experiment proves that the reflex movements of the velum palati, induced by the excitation of the glosso-pharyngeal, are in part transmitted by the facial nerve, the movements of the pillars not being produced by filaments belonging to this nerve."

Bernard also noted a fact, which has sometimes been observed in cases of facial paralysis, that the point of the tongue is deviated after section of the facial; which is explained by the presence of a filament described by Hirschfeld, going from the facial to the tongue.

As we before remarked, the experiments of Bernard do not indicate the mode of communication between the facial and the muscles of the palate. Longet regards the filaments of the facial which influence the levator palati and azygos uvulæ muscles as derived from the large petrosal branch of the nerve, passing to the muscles through Meckel's ganglion, the filaments to the palato-glossus and the palato-pharyngeus being given off from the glosso-pharyngeal, but originally coming from an anastomosing branch of the facial. As regards the branches of communication from the glosso-pharyngeal, Longet mentions a preparation by Richet, in the museum of the *École de médecine*, of Paris, in which branches of the facial upon one side passed directly to the palato-glossus and the palato-pharyngeus, without any connection with the glosso-pharyngeal nerve. In our anatomical description of the branches of the facial, we have already noted a filament, described by Hirschfeld, which passes to the stylo-glossus and palato-glossus muscles. This is the filament affected in deviation of the point of the tongue.

In view of the pathological examples of paralysis of the palate and uvula in certain cases of facial palsy, the frequent occurrence of contractions of the muscles of these parts upon galvanization of the facial, and the reflex action through the glosso-pharyngeal and the facial, there can be little doubt that the muscles of the palate and uvula are animated by filaments derived from the seventh nerve. The effects of paralysis of these muscles are manifested by more or less difficulty in deglutition and in the pronunciation of certain words, with great difficulty in the expulsion of mucus collected in the back part of the mouth and the pharynx.

Functions of the External Branches of the Facial.—The general function of the branches of the facial going to the superficial muscles of the face is sufficiently evident, in view of our present knowledge of the distribution of these branches and the general properties of the nerve. Throughout the writings of Sir Charles Bell, the facial is spoken of as the "respiratory nerve of the face." It is now recognized as the nerve which presides over the movements of the superficial muscles of the face, not including those directly concerned in the act of mastication. This being its general function, it is easy to assign to each of what may be termed the external branches of the facial its particular office.

Just after the facial nerve has passed out at the stylo-mastoid foramen, it sends to the glosso-pharyngeal the communicating branch, the functions of which we have just considered in connection with the movements of the palate.

The posterior auricular branch, becoming sensitive by the addition of filaments from the cervical plexus, gives sensibility to the integument on the back part of the ear and over the occipital portion of the occipito-frontalis muscle. It animates the retrahens and the attollens aurem, muscles but little developed in man, but very important in certain of the inferior animals. It also animates the posterior portion of the occipito-frontalis muscle.

The branches distributed to the posterior belly of the digastric and to the stylo-hyoid muscle simply animate these muscles, one of the uses of which is to assist in deglutition. The same may be said of the filaments that go to the stylo-glossus.

The two great branches distributed upon the face after the trunk of the nerve has passed through the parotid gland have the most prominent function. Both of these branches are somewhat sensitive, from their connections with other nerves, and are distributed in small part to integument.

The temporo-facial branch animates all of the muscles of the upper part of the face. In complete paralysis of this branch, the eye is constantly open, even during sleep, from paralysis of the orbicularis muscle. In cases of long standing, the globe of the eye may become inflamed from constant exposure, from abolition of the movements of winking by which the tears are distributed over its surface and little foreign particles are removed, and, in short, from absence of the protective action of the lids. In these cases, the lower lid may become slightly everted. The frontal portion of the occipito-frontalis, the attrahens aurem, and the corrugator supercilii muscles, are also paralyzed. The most prominent symptom of paralysis of these muscles is inability to corrugate the brow upon one side, as in frowning.

Paralysis of the muscles that dilate the nostrils has been shown to have an important influence upon respiration through the nose. It was the synchronism between the acts of dilatation of the nostrils and the movements of inspiration which first led Sir Charles Bell to regard the facial as a respiratory nerve. In instances of complete paralysis of the nostril of one side, there is frequently some difficulty in inspiration. Sir Charles Bell refers to a case in which, when "the patient lay with the sound side against the pillow, he was under the necessity of holding the paralytic nostril open with the fingers, in order to breathe freely." In the horse, the movements of the nostrils are essential to respiration, the animal being unable to breathe through the mouth. When both facial nerves are divided in this animal, the nostrils collapse and are occluded with each effort at inspiration, and death takes place from suffocation.

Sir Charles Bell and others have also noted an interference with olfaction, due to the inability to inhale with one nostril, in cases of facial paralysis. The influence of the nerve in the act of conveying odorous emanations to the olfactory membrane is sufficiently evident after what we have remarked concerning the action of the facial in respiration.

The effects of paralysis of the other superficial muscles of the face are manifested in the distortion of the features, from the unopposed action of the muscles upon the sound side; a phenomenon which is sufficiently familiar to the practical physician. When facial palsy affects one side and is complete, the angle of the mouth is drawn to the opposite side, the eye upon the affected side is widely and permanently opened even during sleep, and the face has upon that side a peculiarly expressionless appearance. When a patient affected in this way smiles or attempts to grimace, the distortion is much increased. The lips are paralyzed upon one side, which sometimes causes a flow of saliva from the corner of the mouth. In the lower animals that use the lips in prehension, paralysis of these parts interferes considerably with the taking of food. The flaccidity of the paralyzed lips and cheek in the human subject sometimes causes a puffing movement with each act of expiration, as if the patient were smoking a pipe.

FIG. 203.

FIG. 204.

FIG. 205.

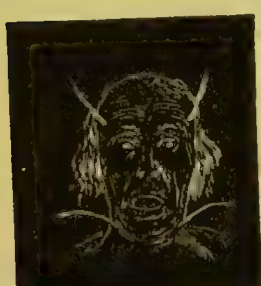


FIG. 206.

FIG. 207.

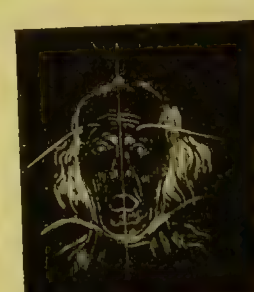


FIG. 208.

Expressions of the face produced by contraction of the muscles under electrical excitation. (Le Bon, after Duchenne.)

Fig. 203, front view of the face in repose.
Fig. 204, profile view.
Fig. 205, expression of laughter upon one side, produced by contraction of the zygomaticus major.
Fig. 206, expression of fear, produced by contraction of the frontal muscle and the depressors of the lower jaw.
Fig. 207, expression of fear, profile view.
Fig. 208, expression of fear and great pain, produced by contraction of the corrugator supercilii and the depressors of the lower jaw.

We have already seen that the buccinator is not supplied by filaments from the nerve of mastication, but is animated solely by the facial. Paralysis of this muscle interferes materially with mastication, from a tendency to accumulation of the food between the teeth and the cheek. Patients complain of this difficulty, and they sometimes keep the food between the teeth by pressure with the hand. In the rare instances in which both facial nerves are paralyzed, there is very great difficulty in mastication, from the cause just mentioned.

The functions of the external branches of the facial are thus sufficiently simple; and it is only as its deep branches affect the taste, the movements of deglutition, etc., that it is difficult to ascertain their exact office. As this is the nerve of expression of the face, it is in the human subject that the phenomena attending its paralysis are most prominent. When both sides are affected, the appearance is most remarkable, the face being absolutely expressionless and looking as if it had been covered with a mask.

Spinal Accessory and Sublingual Nerves.

A description of the properties and functions of the spinal accessory and the sublingual completes the physiological history of the motor nerves emerging from the cranial cavity. The functions of these nerves are important, and, in the case of the spinal accessory, they possess considerable interest, from the fact that physiological investigations have, only within a few years, determined the significance of certain of its anatomical relations. As we have done in studying the other motor nerves, we shall treat successively of their anatomical relations, general properties and functions.

Spinal Accessory Nerve. (*Third Division of the Eighth Nerve.*)

The spinal accessory nerve, from the remarkable extent of its origin, its important anastomoses with other nerves, and its curious course and distribution, has long engaged the attention of anatomists and physiologists, who have advanced many theories with regard to its office. We shall content ourselves, however, with a simple description of its anatomy as it appears from late researches, and shall begin its physiological history with comparatively recent experiments, which alone have advanced our positive knowledge of its properties.

Physiological Anatomy of the Spinal Accessory.—The origin of this nerve is very extensive. A certain portion arises from the lower half of the medulla oblongata, and the rest takes its origin below, from the upper two-thirds of the cervical portion of the spinal cord. That portion of the root which arises from the medulla oblongata is called, by the French, the bulbar portion, the roots from the cord constituting the spinal portion. Inasmuch as there is a marked difference between the functions of these two portions, the anatomical distinction just mentioned is important.

The superior roots arise by four or five filaments from the lower half of the medulla oblongata, below the origin of the pneumogastrics. These filaments of origin, in preparations hardened by prolonged immersion in alcohol, are shown to be connected with the lateral portion of the medulla, and not with the posterior columns. Their origin seems, therefore, to be from the motor tract.

The spinal portion of the nerve arises from the upper part of the cervical division of the spinal cord, between the anterior and posterior roots of the upper four or five cervical nerves. The filaments of origin are from six to eight in number. The most inferior of these is generally single, the other filaments being frequently arranged in pairs. These take their origin from the lateral portion of the cord, rather nearer the posterior median line than the roots from the medulla oblongata.

Following the nerve from its most inferior filament of origin upward, it gradually increases in size by union with its other roots, enters the cranial cavity by the foramen magnum, and passes to the jugular foramen, by which it emerges, in connection with the glosso-pharyngeal, the pneumogastric, and the internal jugular vein.

In its course, the spinal accessory anastomoses with several nerves. Just as it enters the cranial cavity, it receives filaments of communication from the posterior roots of the upper two cervical nerves. These filaments, however, are not constant. It frequently, though not constantly, sends a few filaments to the superior ganglion, or the ganglion of the root of the pneumogastric. After it has emerged by the jugular foramen, it sends a branch of considerable size to the pneumogastric, from which nerve it also receives a few filaments of communication. This branch will be again referred to in connection with the distribution of the nerve. In its course, it also receives filaments of communication from the anterior branches of the second, third, and fourth cervical nerves.

In its distribution, the spinal accessory presents two branches. The first, or anastomotic branch, passes to the pneumogastric just below the plexiform enlargement which is sometimes called the ganglion of the trunk of the pneumogastric.

The internal, or anastomotic branch, is composed principally, if not entirely, of the filaments that take their origin from the medulla oblongata. As it joins the pneumogastric, it subdivides into two smaller branches. The first of these forms a portion of the pharyngeal branch of the pneumogastric. The second becomes intimately united with the pneumogastric, lying at its posterior portion, and furnishes filaments to the inferior, or recurrent laryngeal branch, which is distributed to all of the muscles of the larynx except the crico-thyroid. The passage of the filaments from the spinal accessory to the pharyngeal branch of the pneumogastric is easily observed; but the fact that filaments from this nerve pass to the larynx by the recurrent laryngeal has been ascertained only by physiological experiments.

Fig. 209.—*Spinal accessory nerve.* (Hirschfeld.)
1, trunk of the facial nerve; 2, 2, glosso-pharyngeal nerve; 3, 3, pneumogastric; 4, 4, 4, *trunk of the spinal accessory*; 5, sublingual nerve; 6, superior cervical ganglion; 7, 7, anastomosis of the first two cervical nerves; 8, carotid branch of the sympathetic; 9, 10, 11, 12, 13, branches of the glosso-pharyngeal; 14, 15, branches of the facial; 16, otic ganglion; 17, auricular branch of the pneumogastric; 18, *anastomosing branch from the spinal accessory to the pneumogastric*; 19, anastomosis of the first pair of cervical nerves with the sublingual; 20, *anastomosis of the spinal accessory with the second pair of cervical nerves*; 21, *pharyngeal plexus*; 22, superior laryngeal nerve; 23, external laryngeal nerve; 24, middle cervical ganglion.

The external, or large branch of the spinal accessory, called the muscular branch, penetrates and passes through the posterior portion of the upper third of the sterno-cleido-mastoid muscle, goes to the anterior surface of the trapezius, which muscle receives its ultimate branches of distribution. In its passage through the sterno-cleido-mastoid, it joins with branches from the second and third cervical nerves and sends filaments of distribution to the muscle. Although the two muscles just mentioned receive numerous motor filaments from the spinal accessory, they are also supplied from the cervical nerves; and, consequently, they are not entirely paralyzed when the spinal accessory is divided.

Properties and Functions of the Spinal Accessory.—Notwithstanding the great difficulty in exposing and in operating upon the roots of the spinal accessory, it has been demonstrated that their galvanization produces convulsive movements in certain muscles. The most satisfactory experiments with relation to the general properties of the roots were made by Bernard. This physiologist cut through the occipito-atloid membranes and galvanized the filaments within the spinal canal. By galvanizing the filaments arising from the medulla oblongata, he produced contractions of the muscles of the pharynx and larynx and no movements of the sterno-mastoid and trapezius. Galvanization of the roots arising from the spinal cord produced movements of the two muscles just mentioned and absolutely no movements in the larynx. In view of these experiments, it is evident that the true filaments of origin of the spinal accessory are motor; and it is farther evident that the filaments from the medulla oblongata are distributed to the muscles of the pharynx and larynx, while the filaments from the spinal cord go to the sterno-cleido-mastoid and trapezius.

The trunk of the spinal accessory, after the nerve has passed out of the cranial cavity, is endowed with a certain degree of sensibility. If the nerve be divided, the peripheral extremity manifests recurrent sensibility, but the central end is also sensible, probably from direct filaments of communication from the cervical nerves and the pneumogastric. As we have remarked, however, in treating of the properties of some other of the cranial nerves, it is exceedingly difficult to note satisfactorily a slight degree of sensibility in nerves that can be exposed only by a tedious and painful operation.

The functions of the external, or muscular branch of the spinal accessory are sufficiently evident; and the effects of the destruction of the nerves on both sides, as far as this branch is concerned, simply resolve themselves into the phenomena due to partial paralysis of the sterno-mastoid and trapezius; but the functions of the branch which joins the pneumogastric are much more complex.

Functions of the Internal Branch from the Spinal Accessory to the Pneumogastric.—Bischoff attempted to ascertain the functions of this branch by dividing the roots of the spinal accessory upon both sides in a living animal. The results of his experiments may be stated in a very few words: He attempted to divide all of the roots of the nerves upon both sides by dissecting down to the occipito-atloid space and penetrating into the cavity of the spinal canal. In the first three experiments upon dogs, the animals died so soon after section of the nerves, that no satisfactory results were obtained. In two succeeding experiments upon dogs, the animals recovered. After division of the nerves, the voice became hoarse, but a few weeks later, it became normal. On killing the animals, an examination of the parts showed that some of the filaments of origin had not been divided. An experiment was then made upon a goat, but this was unsatisfactory, as the roots were not completely divided. Finally, another experiment was made upon a goat. In this the results were more satisfactory. After division of the nerve upon one side, the voice became hoarse. As the filaments were divided upon the opposite side, the voice was enfeebled, until finally it became extinct. The sound emitted afterward was one which could in nowise be called voice ("*qui neutiquam vox appellari potuit*"). This experiment was made in the presence of Tiedemann and Seubertus and was not repeated.

Bernard, whose ingenious experiments determined exactly the influence of the spinal accessory over the vocal movements of the larynx, first repeated the experiments of Bischoff; but the animals operated upon died so soon, from hæmorrhage or other causes, that his observations were not satisfactory. After many unsuccessful trials, he succeeded in overcoming all difficulties, by following the trunk of the nerve back to the jugular foramen, seizing it here with a strong pair of forceps, and drawing it out by the roots. This operation is difficult, but we have several times performed it with entire success, and have verified, in every regard, the facts observed by Bernard. Within the last year, the excellent assistant to the chair of Physiology at the Bellevue Hospital Medical College, Dr. C. F. Roberts, has succeeded in extirpating these nerves for class-demonstrations. The operation is generally most successful in cats, although Bernard has succeeded frequently in other animals.

The operative procedure employed by Bernard is the following: The trunk of the nerve is exposed as it passes through the sterno-cleido-mastoid muscle. It is then followed up by careful dissection, avoiding blood-vessels as much as possible, to the posterior foramen lacerum, when the sublingual is seen crossing the course of the pneumogastric. It is here that the anastomotic branch leaves the spinal accessory to go to the pneumogastric. At this point, the external branch, with the anastomosing branch, is seized with a pair of rather broad-billed forceps, and gentle but firm traction is applied to the entire nerve. Soon there is a cracking sensation conveyed to the hand as the roots give way, and the nerve may then be drawn out entire. With care, either the filaments of origin from the medulla or those from the cord may be extirpated alone.

When one spinal accessory is extirpated, the vocal sounds are hoarse and unnatural. When both nerves are torn out, in addition to the disturbance of deglutition and the partial paralysis of the sterno-mastoid and trapezius muscles, the voice becomes extinct. Animals operated upon in this way move the jaws and make evident efforts to cry, but no vocal sound is emitted. This condition is very striking; and, inasmuch as Bernard has kept animals, with both nerves extirpated, for months, the question of the function of these nerves in phonation may now be regarded as definitively settled.

It remains now to consider the experimental facts with regard to the influence of the different filaments of origin of the spinal accessory upon the voice. These are simple and entirely conclusive; and they are due exclusively to the researches of Bernard. This experimenter found that division of the roots of origin from the spinal cord not only did not affect the voice, but sometimes it seemed to render it clearer; but that division of the roots of origin from the medulla oblongata abolished the voice, although the inferior roots were intact.

It is not necessary to discuss the action of the muscles of the larynx in phonation, as this subject has already been considered in connection with the voice. The experiments that have demonstrated the influence of the spinal accessory nerve over these muscles have pointed out the destination of the fibres that join the pneumogastric, which could never have been done so satisfactorily by dissection. They have shown farther that the movements involved in phonation are more or less independent of the respiratory movements of the larynx.

If the larynx be exposed in a living animal, with all its nervous connections intact, it will be seen to open widely during inspiration, being passive in expiration. The wide opening of the glottis at this time is due to the fact that, after the operation, respiration is usually more or less labored; but, if we carefully observe the parts when the respiratory acts are perfectly tranquil, the movements of the glottis seem to be very slight. The larynx is then permanently opened to a moderate degree, but the chink of the glottis is slightly dilated with each expiration. If the recurrent laryngeal nerves, which are distributed to all of the muscles of the larynx except the crico-thyroid, be now divided upon both sides, the larynx is entirely paralyzed, and in cats and young animals, in which the cartilages are soft and flexible, the parts are occluded by the effort of inspiration, and death takes place from suffocation. Of course the division of the recurrent laryngeal nerves abolishes the voice, but it arrests the other movements of the larynx as well. The distinction thus established between the action of the spinal accessory and of the recurrent laryngeal nerves was fully illustrated by Bernard, in the following experiments:

In a cat, in which the voice had been completely destroyed by extirpation of both spinal accessory nerves, the larynx was exposed. The glottis was seen dilated so as to permit the free passage of air in respiration. The mucous membrane retained its sensibility, and, when the interior of the larynx was irritated, a very slight but ineffectual effort was made to close the glottis. It was impossible for the animal to approximate the posterior points of attachment of the vocal cords or to put the cords upon the stretch. If such irritation be applied to the larynx of an animal with the spinal accessory nerves intact, the glottis is instantly and firmly closed.

In a cat about five weeks old, both spinal accessory nerves were extirpated, and the voice was thus destroyed. Two days after, both recurrent laryngeal nerves were divided, and the animal died almost immediately of suffocation.

These experiments show conclusively that the internal, or communicating branch of the spinal accessory is the nerve which presides over the movements of the larynx in phonation. The filaments undoubtedly pass to the larynx in greatest part through the recurrent laryngeal branches of the pneumogastric; but the recurrent laryngeals also contain motor filaments from other sources, which latter are chiefly concerned in the respiratory movements of the glottis.

Influence of the Internal Branch of the Spinal Accessory upon Deglutition.—There are two ways in which deglutition is affected through this nerve: 1. When the larynx is paralyzed as a consequence of extirpation of both nerves, the glottis cannot be completely closed to prevent the entrance of foreign bodies into the air-passages. In rabbits particularly, it has been noted that particles of food penetrate the trachea and find their way into the lungs. 2. The spinal accessory furnishes numerous filaments to the pharyngeal branch of the pneumogastric, and, through this nerve, it directly affects the muscles of deglutition; but the muscles animated in this way by the spinal accessory have a tendency to draw the lips of the glottis together, while they assist in passing the alimentary bolus into the œsophagus. When these important acts are wanting, there is some difficulty in the process of deglutition itself as well as danger of the passage of foreign particles into the larynx.

Influence of the Spinal Accessory upon the Heart.—When we come to study the varied functions of the pneumogastrics, we shall discuss fully the mechanism by which the contractions of the heart are arrested by galvanization of both of these nerves in the neck. A very curious and interesting observation by Waller has demonstrated that this influence, whatever be its mechanism, is derived from the spinal accessory and necessarily comes through its communicating branch. It has been found that a powerful current of galvanism passed through the pneumogastric upon one side will arrest the action of the heart. Waller found that, if he extirpated the spinal accessory upon one side, the action of the heart could not be arrested by galvanizing the pneumogastric upon the same side; but this result followed galvanization of the pneumogastric upon the opposite side, on which the connections with the spinal accessory were intact. These phenomena, however, could not be observed until from ten to twelve days had elapsed after the extirpation of the spinal accessory. We have already seen, in treating of the general properties of the nerves, that the irritability of the motor nerves disappears in about four days after their separation from the nerve-centres. In the observation just referred to, it seemed necessary that a sufficient time should elapse after extirpation of the spinal accessory for the irritability of the filaments that join the pneumogastric to become extinct; but the experiment is sufficient to show the direct inhibitory influence of the spinal accessory upon the heart. This subject will be more fully considered, however, in connection with the functions of the pneumogastrics.

Functions of the External, or Muscular Branch of the Spinal Accessory.—The most interesting feature in the recent researches into the functions of the spinal accessory is, that experimentalists have been able to separate physiologically the internal from the external branch. Observations have conclusively demonstrated that the internal branch, and the internal branch only, is directly concerned in the vocal movements of the larynx, and, to a great extent, in the closure of the glottis during deglutition. It has been noted, in addition, that animals in which both branches have been extirpated present irregularity of the movements of the anterior extremities and suffer from shortness of breath after violent muscular exertion. The use of the corresponding extremities in the human subject is so different, that it is not easy to make a direct application of these experiments; still, we can draw from them certain inferences with regard to the functions of the external branch in man.

In prolonged vocal efforts, the vocal cords are put upon the stretch, and the act of expiration is very different from that in tranquil breathing. In singing, for example, the shoulders are frequently fixed; and this is done to some extent by the action of the sterno-cleido-mastoid and the trapezius. We may suppose, then, that the action of the branch of the spinal accessory which goes to these muscles has a certain synchronism with the action of the branch going to the larynx and the pharynx; the one fixing the upper part of the chest so that the expulsion of the air through the glottis may be more nicely regulated by the expiratory muscles, and the other acting upon the vocal cords.

In what is known to physiologists as muscular effort, the glottis is closed, the thorax is fixed after a full inspiration, and respiration is arrested so long as the effort, if it be not too prolonged, is continued. The same synchronism, therefore, obtains in this as in prolonged vocal efforts. In experiments in which the muscular branch only has been divided, shortness of breath, after violent muscular effort, is observed; and this is probably due to the want of synchronous action of the sterno-cleido-mastoid and trapezius. The irregularity in the movements of progression in animals, in which either both branches or the muscular branches alone have been divided, is due to anatomical peculiarities. Bernard has observed these irregularities in the dog and the horse, but they are not so well marked in the cat. There have been no opportunities for illustrating these points in the human subject.

Sublingual, or Hypoglossal Nerve. (*Ninth Nerve.*)

The last of the motor cranial nerves is the sublingual; and its functions are intimately connected with the physiology of the tongue in deglutition and articulation, although it is also distributed to certain of the muscles of the neck.

Physiological Anatomy of the Sublingual Nerve.—The apparent origin of the sublingual is from the medulla oblongata, in the groove between the olivary body and the anterior pyramid, on the line of the anterior roots of the spinal nerves. At this point, its root is formed of from ten to twelve filaments, which extend from the inferior portion of the olivary body to about the junction of the upper with the middle third. These filaments of origin are separated into two groups, superior and inferior. From this apparent origin, the filaments have been traced into the gray matter of the floor of the fourth ventricle, between the deep origin of the pneumogastric and the glosso-pharyngeal. Although there is much difference of opinion upon this point, it is probable that some of the filaments of origin of these nerves decussate in the floor of the fourth ventricle. The superior and inferior filaments of origin of the nerve unite to form two bundles, which pass through distinct perforations in the dura mater. These two bundles then pass into the anterior condyloid foramen and unite into a single trunk as they emerge from the cranial cavity.

After the sublingual has passed out of the cranial cavity, it anastomoses with several nerves. It sends a filament of communication to the sympathetic as it branches from the superior cervical ganglion. Soon after it has passed through the foramen, it sends a branch to the pneumogastric. It anastomoses by two or three branches with the upper two cervical nerves, the filaments passing in both directions between the nerves. It anastomoses with the lingual branch of the fifth, by two or three filaments passing in both directions.

In its distribution, the sublingual presents several remarkable peculiarities:

Its first branch, the descendens noni, passes down the neck to the sterno-hyoid, sterno-thyroid, and omo-hyoid muscles. From its relations with important vessels and nerves, this branch possesses considerable surgical interest.

The thyro-hyoid branch is distributed to the thyro-hyoid muscle.

The other branches are distributed to the stylo-glossus, hyo-glossus, genio-hyoid, and genio-hyo-glossus muscles, their terminal filaments going to the intrinsic muscles of the tongue.

It is thus seen that the sublingual nerve is distributed to all of the muscles in the infra-hyoid region, the action of which is to depress the larynx and the hyoid bone after the passage of the alimentary bolus through the pharynx; to one of the muscles in the supra-hyoid region, the genio-hyoid; to most of the muscles which move the tongue; and to the muscular fibres of the tongue itself. The action of these muscles and of the tongue itself in deglutition has already been fully discussed.

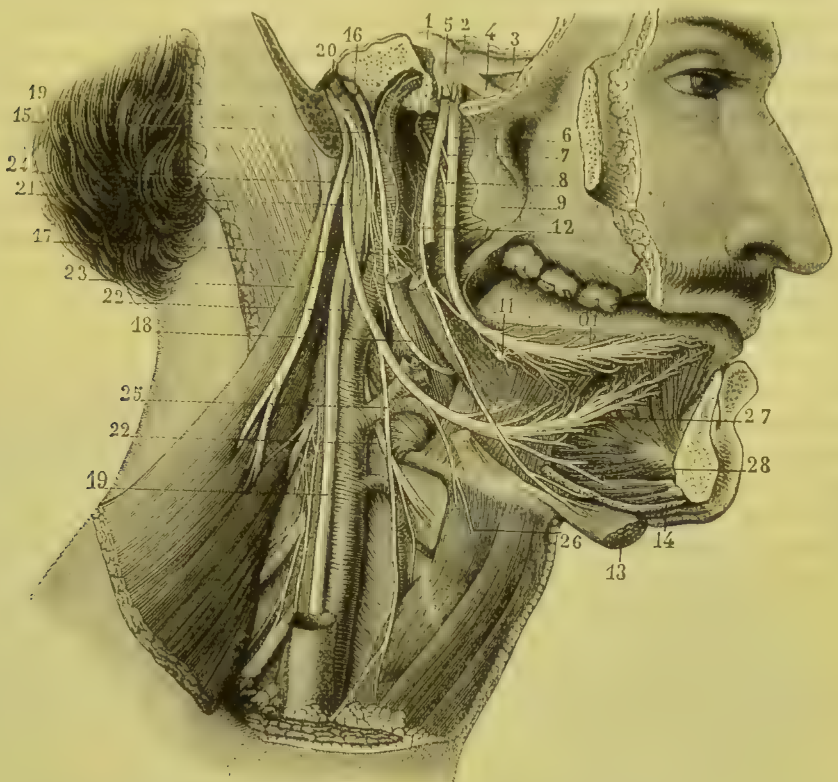


FIG. 210.—*Distribution of the sublingual nerve.* (Sappey.)

1, root of the fifth nerve; 2, ganglion of Gasser; 3, 4, 5, 6, 7, 9, 10, 12, branches and anastomoses of the fifth nerve; 11, submaxillary ganglion; 13, anterior belly of the digastric muscle; 14, section of the mylo-hyoid muscle; 15, glosso-pharyngeal nerve; 16, ganglion of Andersch; 17, 18, branches of the glosso-pharyngeal nerve; 19, 19, pneumogastric; 20, 21, ganglia of the pneumogastric; 22, 22, superior laryngeal branch of the pneumogastric; 23, spinal accessory nerve; 24, *sublingual nerve*; 25, *descendens noni*; 26, *thyro-hyoid branch*; 27, *terminal branches*; 28, *two branches, one to the genio-hyo-glossus and the other to the genio-hyoid muscle.*

Properties and Functions of the Sublingual.—There is every reason to believe that the sublingual nerve is entirely insensible at its origin from the medulla oblongata. The fact that it arises from a continuation of the motor tract of the spinal cord and has no ganglion upon its main root would lead to the supposition that it is an exclusively motor nerve. In operating upon the roots of the spinal accessory, when the origin of the sublingual is necessarily exposed, Longet has irritated the roots in the dog, without any evidence of pain on the part of the animal. Such experiments, taken in connection with the anatomical characters of the nerve, render it almost certain that its root is devoid of sensibility at its origin. All modern experimenters have confirmed the observations of Mayo and of Magendie, with regard to the sensibility of the sublingual after it has passed out of the cranial cavity. The anastomoses of this nerve with the upper two cervical nerves, with the pneumogastric, and with the lingual branch of the fifth, afford a ready explanation of this fact.

The functions of the sublingual have already been so fully considered under the head of deglutition, that they need not be discussed elaborately in this connection. We shall here simply state the phenomena which follow stimulation of the nerve and the division of both nerves in living animals.

The sublingual may be easily exposed in the dog by making an incision just below the border of the lower jaw, dissecting down to the carotid artery and following the vessel upward until we see the nerve as it crosses its course. On applying a feeble current of galvanism at this point, there are evidences of sensibility, and the tongue is moved convulsively at each stimulation.

The phenomena following section of both sublingual nerves point directly to their function. The most notable fact observed after this operation is, that the movements of the tongue are entirely lost, while general sensibility and the sense of taste are not affected. The phenomena which follow division of these nerves consist simply in loss of power over the tongue, with considerable difficulty in deglutition. We have repeatedly noted all of these points and have demonstrated them to medical classes.

In the human subject, the sublingual is usually more or less affected in hemiplegia. In these cases, as the patient protrudes the tongue the point is deviated. This is due to the unopposed action of the genio-hyo-glossus upon the sound side, which, as it protrudes the tongue, directs the point toward the side affected with paralysis.

A disease of rather rare occurrence has lately been described under the name of glosso-labial paralysis, which is characterized by paralysis of the sublinguals, affecting also the orbicularis oris and frequently the intrinsic muscles of the larynx. The phenomena referable to the loss of power over the tongue correspond to those observed in animals after section of the sublingual nerves. Patients affected in this way experience difficulty in deglutition, and, in addition, we note an interference with articulation, which cannot be observed in experiments upon animals. We lately had a case of this disease under observation in the Bellevue Hospital, the phenomena of which were peculiarly interesting from a physiological point of view. This patient presented complete paralysis of the tongue, with considerable difficulty in deglutition, probably from the tongue-affection. The orbicularis oris was also paralyzed. The paralysis probably extended to the intrinsic muscles of the larynx, as little or no vocal sound could be made. The patient was incapable of articulate language and communicated entirely by signs.

CHAPTER XIX.

SENSORY CRANIAL NERVES.

Trifacial, or trigeminal nerve—Physiological anatomy of the trifacial—Properties and functions of the trifacial—Division of the trifacial within the cranal cavity—Immediate effects of division of the trifacial—Remote effects of division of the trifacial—Division of the trifacial before and behind the ganglion of Gasser—Communication with the sympathetic at the ganglion of Gasser—Explanation of the phenomena of disordered nutrition after division of the trifacial—Cases of paralysis of the trifacial in the human subject—Pneumogastric nerve (second division of the eighth)—Physiological anatomy—Properties and functions of the pneumogastric—General properties of the roots—Properties and functions of the auricular nerves—Properties and functions of the pharyngeal nerves—Properties and functions of the superior laryngeal nerves—Properties and functions of the inferior, or recurrent laryngeal nerves—Properties and functions of the cardiac nerves, and influence of the pneumogastrics upon the circulation—Depressor-nerve of the circulation—Properties and functions of the pulmonary branches, and influence of the pneumogastrics upon respiration—Properties and functions of the œsophageal nerves—Properties and functions of the abdominal branches.

Trifacial, or Trigeminal Nerve. (Large Root of the Fifth Nerve.)

A single nerve, the large root of the fifth pair, called the trifacial or the trigeminal, gives general sensibility to the face and to the head as far back as the vertex. This is one of the most interesting of the cranial nerves and is one of the first that was experimented upon by physiologists. It is interesting, not only as the great sensitive nerve of the face, but from its connections with other nerves and its relations to the organs of special sense. In studying the physiology of this nerve, we must necessarily begin with its physiological anatomy.

Physiological Anatomy of the Trifacial Nerve.—The apparent origin of the large root of the fifth is from the lateral portion of the pons Varolii, posterior and inferior to the origin of the small root, from which it is separated by a few transverse fibres of white substance. The deep origin is far removed from its point of emergence from the encephalon. The roots pass entirely through the substance of the pons, from without inward and from before backward, without any connection with the fibres of the pons itself. By this course, it reaches the medulla oblongata, where the roots divide into three bundles. The anterior bundle passes from behind forward, between the anterior fibres of the pons and the cerebellar portion of the restiform bodies, to anastomose with the auditory nerve. The other bundles, which are posterior, pass, the one in the anterior wall of the fourth ventricle to the lateral tract of the medulla oblongata, and the other, becoming grayish in color, to the restiform bodies, from which they may be followed as far as the point of the calamus scriptorius. A few fibres from the two sides decussate at the median line in the anterior wall of the fourth ventricle. From this origin, the large root of the fifth passes obliquely upward and forward to the ganglion of Gasser, which is situated in a depression in the petrous portion of the temporal bone on the internal portion of its anterior face.

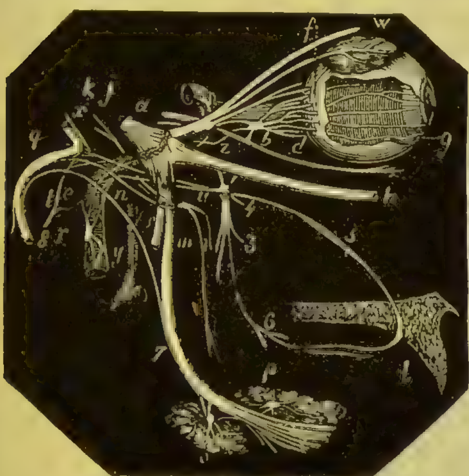


FIG. 211.—*Principal branches of the large root of the fifth nerve.* (Robin.)

a, ganglion of Gasser; a–w, ophthalmic division of the fifth; b, ophthalmic ganglion; c, branch from the ophthalmic division of the fifth to the ophthalmic ganglion; d, motor oculi communis; *e,* carotid; *f,* ciliary nerves; *g,* cornea and iris; *a–h, superior maxillary division of the fifth; i, two branches from the superior maxillary division of the fifth to the spheno-palatine ganglion; j,* deep petrosal nerve; *k,* filaments from the motor root of the fifth to the internal muscle of the malleus; *l,* naso-palatine ganglion; *m,* otic ganglion; *n,* small superficial petrosal nerve; *o, branches of the fifth to the submaxillary ganglion; p, branches to the sublingual ganglion; q,* facial nerve; *r,* sympathetic ganglion; *s,* nerve of mastication; *t, chorda tympani, joining the lingual branch of the fifth; u,* Vidian nerve; *v,* branch from the motor root to the internal pterygoid muscle; *w, branch of the fifth to the lachrymal gland; x,* bend of the facial nerve; *y,* middle meningeal artery; *z,* filament from the carotid plexus to the ophthalmic ganglion; (1 and 2 are not in the figure) 3, external spheno-palatine filaments; 4, spheno-palatine ganglion; 5, naso-palatine nerve; 6, anterior palatine nerve; 7, *inferior maxillary division of the fifth;* 8, nerve of Jacobson.

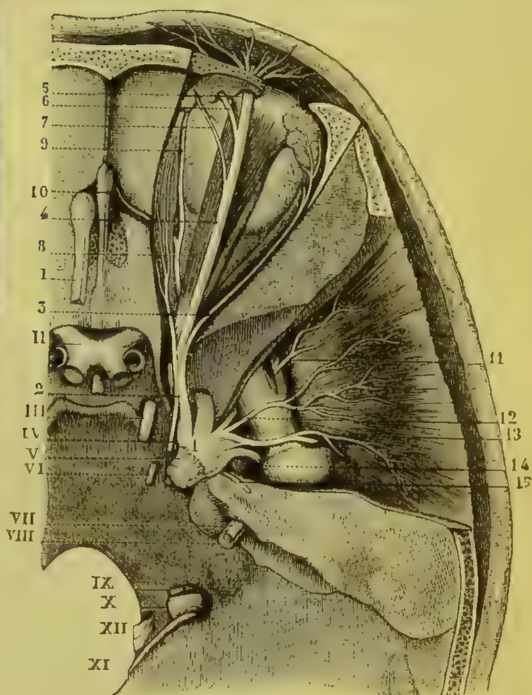


FIG. 212.—*Ophthalmic division of the fifth.* (Hirschfeld.)

1, *ganglion of Gasser;* 2, *ophthalmic division of the fifth;* 3, *lachrymal branch;* 4, *frontal branch;* 5, *external frontal;* 6, *internal frontal;* 7, *supratrochlear;* 8, *nasal branch;* 9, *external nasal;* 10, *internal nasal;* 11, anterior deep temporal nerve; 12, middle deep temporal nerve; 13, posterior deep temporal nerve; 14, origin of the superficial temporal nerve; 15, great superficial petrous nerve.
I to XII, roots of the cranial nerves.

The Gasserian ganglion is semilunar in form (sometimes it is called the semilunar ganglion), with its concavity looking upward and inward. At the ganglion, the nerve receives filaments of communication from the carotid plexus of the sympathetic. This anatomical point is of importance in view of some of the remote effects which follow division of the fifth nerve through the ganglion in living animals.

It will be necessary only to describe in a general way the numerous branches of distribution of the fifth nerve, remembering that it is the great sensitive nerve of the face.

At the ganglion of Gasser, from its anterior and external portion, are given off a few small and unimportant branches to the dura mater and the tentorium.

From the convex border of the ganglion, the three great branches arise, which have given to the nerve the name of trifacial or trigeminal. These are: 1, the ophthalmic; 2, the superior maxillary; 3, the inferior maxillary. The ophthalmic and the superior maxillary branch are derived entirely from the sensory root. The inferior maxillary branch joins with the motor root and forms a mixed nerve.

The ophthalmic branch, the first division of the fifth, is the smallest of the three. Before it enters the orbit, it receives filaments of communication from the sympathetic, sends small branches to all of the motor nerves of the eyeball, and gives off a small recurrent branch which passes between the layers of the tentorium.

Just before the ophthalmic branch enters the orbit by the sphenoidal fissure, it divides into three branches; the lachrymal, frontal, and nasal.

The lachrymal, the smallest of the three, sends a branch to the orbital branch of the superior maxillary nerve, passes through the lachrymal gland, to which certain of its filaments are distributed, and its terminal filaments go to the conjunctiva and to the integument of the upper eyelid.

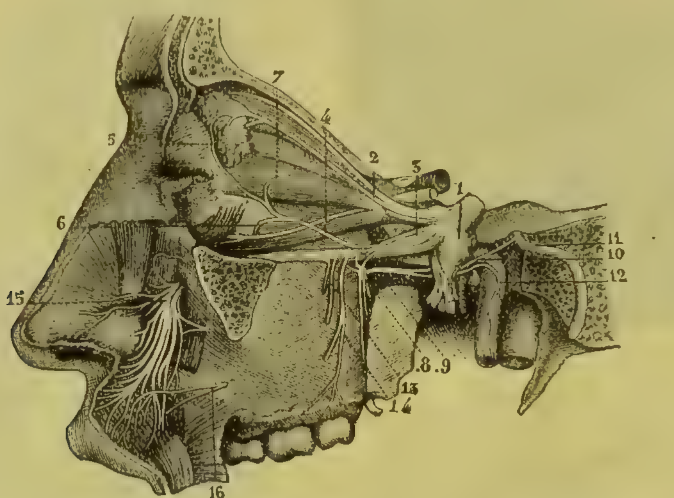


FIG. 213.—*Superior maxillary division of the fifth.* (Hirschfeld.)
1, ganglion of Gasser; 2, lachrymal branch of the ophthalmic division; 3, *superior maxillary division of the fifth*; 4, *orbital branch*; 5, *lachrymo-palpebral filament*; 6, *malar branch*; 7, *temporal branch*; 8, *spheno-palatine ganglion*; 9, Vidian nerve; 10, great superficial petrosal nerve; 11, facial nerve; 12, branch of the Vidian nerve; 13, *anterior and two posterior dental branches*; 14, *branch to the mucous membrane of the alveolar processes*; 15, *terminal branches of the superior maxillary division*; 16, branch of the facial.

The frontal branch, the largest of the three, divides into the supra-trochlear and supra-orbital nerves. The supra-trochlear passes out of the orbit between the supra-orbital foramen and the pulley of the superior oblique muscle. It sends in its course a long, delicate filament to the nasal branch and is finally lost in the integument of the forehead. The supra-orbital passes through the supra-orbital foramen, sends a few filaments to the upper eyelid, and supplies the forehead, the anterior and median portions of the scalp, the mucous membrane of the frontal sinus, and the pericranium covering the frontal and parietal bones.

The nasal branch, before it penetrates the orbit, gives off a long, delicate filament to the ophthalmic ganglion, constituting its sensory root. It then gives off the long ciliary nerves, which pass to the ciliary muscle and iris. Its trunk finally divides into the external nasal, or infra-trochlearis, and the internal nasal, or ethmoidal. The infra-trochlearis is distributed to the integument of the forehead and nose, to the internal surface of the lower eyelid, the lachrymal sac, and the caruncula. The internal nasal is distributed to the mucous membrane, and also in part to the integument of the nose.

The superior maxillary branch of the fifth passes out of the cranial cavity by the foramen rotundum, traverses the infra-orbital canal, and emerges upon the face by the infra-orbital foramen. Branches from this nerve are given off in the spheno-maxillary fossa and the infra-orbital canal, before it emerges upon the face. In the spheno-maxillary fossa, the first branch is the orbital, which passes into the orbit, giving off one branch, the temporal, which passes through the temporal fossa by a foramen in the malar bone and is distributed to the integument on the temple and the side of the forehead. Another branch, the malar, which likewise emerges by a foramen in the malar bone, is distributed to the integument over this bone. In the spheno-maxillary fossa, are also given off two branches, which pass to the spheno-palatine, or Meckel's ganglion. From this portion of the nerve, branches are given off, the two posterior dental nerves, which are distributed to the molar and bicuspid teeth, the mucous membrane of the corresponding alveolar processes, and to the antrum.

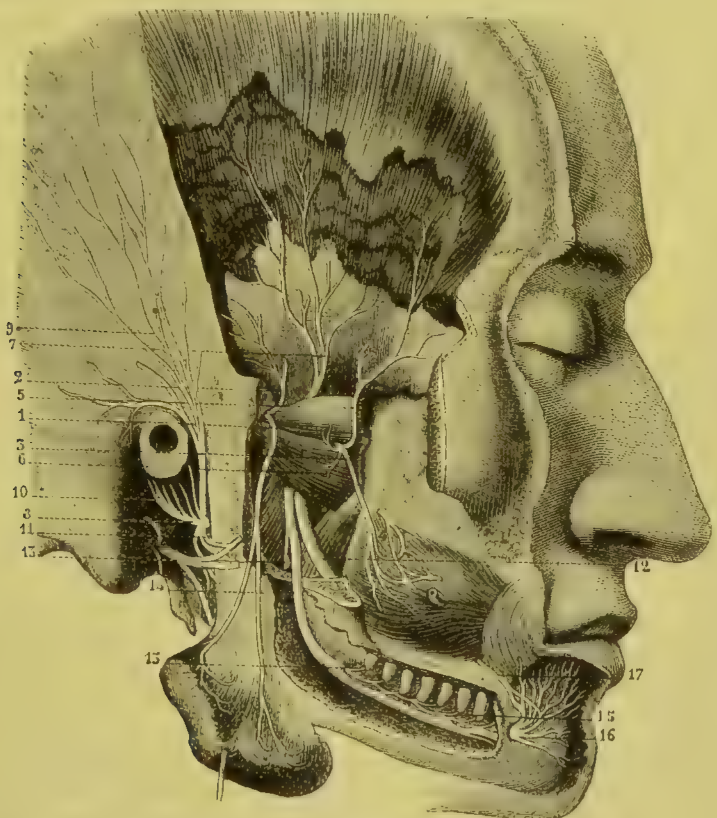


Fig. 214.—*Inferior maxillary division of the fifth.* (Hirschfeld.)
1, branch from the motor root to the masseter muscle; 2, filaments from this branch to the temporal muscle; 3, buccal branch; 5, 6, 7, branches to the muscles; 8, *auriculo-temporal nerve*; 9, *temporal branches*; 10, *auricular branches*; 11, *anastomosis with the facial nerve*; 12, *lingual branch*; 13, branch of the motor root to the mylo-hyoid muscle; 14, 15, 15, *inferior dental nerve, with its branches*; 16, *mental branch*; 17, *anastomosis of this branch with the facial nerve.*

In the infra-orbital canal, a large branch, the anterior dental, is given off to the teeth and mucous membrane of the alveolar processes not supplied by the posterior dental nerves. This nerve anastomoses with the posterior dental.

The terminal branches upon the face are distributed to the lower eyelid (the palpebral branches); to the side of the nose (the nasal branches), anastomosing with the nasal branch of the ophthalmic; and to the integument and mucous membrane of the upper lip (the labial branches).

The inferior maxillary is a mixed nerve, composed of the inferior division of the large root and the entire small root. The distribution of the motor filaments has already been described under the head of the nerve of mastication. This nerve passes out of the cranial cavity by the foramen ovale, and then separates into the anterior division, containing nearly all of the motor filaments, and the posterior division, which is chiefly sensory. The sensory portion breaks up into numerous branches:

1. The auriculo-temporal nerve supplies the integument in the temporal region, the auditory meatus and the integument of the ear, the temporo-maxillary articulation, and the parotid gland. It also sends important branches of communication to the facial.

2. The lingual branch is distributed to the mucous membrane of the tongue as far as the point, the mucous membrane of the mouth, the gums, and to the sublingual gland. This nerve receives an important branch from the facial (the chorda tympani) which has already been described. From this nerve, also, are given off two or three branches which pass to the submaxillary ganglion, constituting its sensory roots.

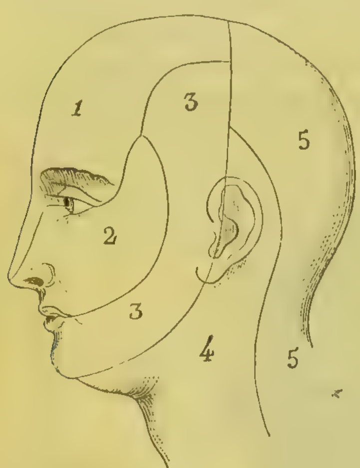


Fig. 215.—*Limits of cutaneous distribution of sensory nerves to the face, head, and neck.* (Béclard.)

1, cutaneous distribution of the ophthalmic division of the fifth; 2, distribution of the superior maxillary division; 3, 3, distribution of the inferior maxillary division; 4, distribution of the anterior branches of the cervical nerves; 5, 5, distribution of the posterior branches of the cervical nerves.

3. The inferior dental nerve, the largest of the three, passes in the substance of the inferior maxillary bone, beneath the teeth, to the mental foramen, where it emerges upon the face. The most important sensory branches are those which supply the pulps of the teeth, and the branches upon the face. The nerve, emerging upon the face by the mental foramen, called the mental nerve, supplies the integument of the chin and the lower part of the face, the lower lip, and sends certain filaments to the mucous membrane of the mouth.

Properties and Functions of the Trifacial.—In 1822, Herbert Mayo published an account of "experiments to determine the influence of the portio dura of the seventh, and of the facial branches of the fifth pair of nerves." These experiments consisted in dividing the infra-orbital, inferior maxillary and frontal branches of the fifth, and the branch from the fifth to the seventh, in asses, by which it was demonstrated that these were exclusively sensory nerves. In a second publication, the following year, it is stated that the root of the fifth was divided in the cranial cavity in pigeons; but this was with reference chiefly to the movements of the iris, although Mayo notes that after division of the nerve "the surface of the eyeball appears to have lost its feeling."

In 1823, Foděra published an account of experiments in which he had divided the roots of the fifth in living animals (rabbits) by introducing a small knife through an opening in the parietal bone, along the base of the skull, and cutting through the roots near the Gasserian ganglion. The operation was followed by complete loss of sensibility upon the side on which the nerve had been divided. In this and other experiments, however, the animals died a short time after the operation. The paper in which these experiments were detailed was presented to the Academy of Sciences, December 31, 1822, and was published at about the same time as the experiments of Mayo.

In 1824, Magendie published an account of his experiments upon the fifth pair. He divided the nerve at its root, by introducing a small stylet through the skull, and noted immediate loss of sensibility upon the corresponding side of the face. Magendie was the first to succeed in keeping the animals alive, observing certain interesting remote effects following division of the nerve.

The operative procedure employed by Magendie has been followed, with great success, by other physiologists, particularly Bernard, to whose researches we are indebted for many additional facts of interest concerning the functions of the fifth nerve. As this is an operation which we have frequently performed with success, following the minute directions laid down by Bernard, we shall quote from him in brief the different steps:

The nerve may be divided in the cranial cavity with tolerable certainty in rabbits, cats, dogs, and Guinea-pigs, but it is most easily done in rabbits. The operation is difficult from the fact that one is working in the dark, and it requires a certain amount of dexterity, to be acquired only by practice. The instrument used is represented in Fig. 216. The operative procedure is as follows:

1. "The head of the rabbit is firmly held in the left hand. The operator feels with the finger of the right hand the tubercle situated in front of the ear, formed by the condyle of the lower jaw. Behind this tubercle, is a hard, osseous portion, the origin of the auditory canal.

2. "The operator penetrates just behind the superior border of the condyle, directing the point of the instrument slightly forward to avoid passing into the substance of the petrous portion of the temporal bone, and thus passes more easily into the middle temporal fossa; at the same time the instrument is directed a little upward to avoid slipping into the zygomatic fossa and thus failing to enter the cranial cavity.

3. "As soon as the instrument has penetrated the cranium, which is recognized by the point becoming free, the pressure is arrested and the instrument is directed downward and backward, its back sliding along the anterior face of the bone, which should serve as a guide in the operation.

4. "This point of departure—that is to say, the anterior face of the bone—being found, the instrument is pushed along, following its inferior border and proceeding gradually, as the instrument penetrates, pressing on the bone, the resistance of which can be easily recognized. Soon, however, the operator feels, at a certain depth, that the bony resistance ceases: he is then on the fifth pair, and the cries of the animal give evidence that the nerve is pressed upon.

FIG. 216.—*Instrument for dividing the fifth nerve.* (Bernard.)

5. "It is at this moment that it is necessary to hold firmly the instrument and the head of the animal; then the cutting edge is turned so as to be directed downward and backward, at the same time pressing in this direction so as to divide the nerve on the extremity of the petrous portion, behind the ganglion of Gasser, if possible, or at least on the ganglion itself.

6. "The instrument is then drawn back, pressing upon the bone so as to accomplish completely the section of the trunk of the fifth pair; then it is withdrawn by passing over the same course on the anterior face of the petrous portion so as not to lacerate the cerebral substance.

"The accident to be feared in the operation is section of the carotid when the instrument has penetrated too far, or lesion of the cavernous sinus when it is pressed too far forward."

When this operation has been performed without accident, its immediate effects are very striking. The cornea and the integument and mucous membrane upon that side of the head are instantaneously deprived of sensibility and may be pricked, lacerated, or burned, without the slightest evidence of pain on the part of the animal. Almost always the small root of the fifth is divided as well as the large root, and the muscles of mastication are paralyzed upon one side; but, with this exception, there is no paralysis of motion, sensation alone being destroyed upon one side.

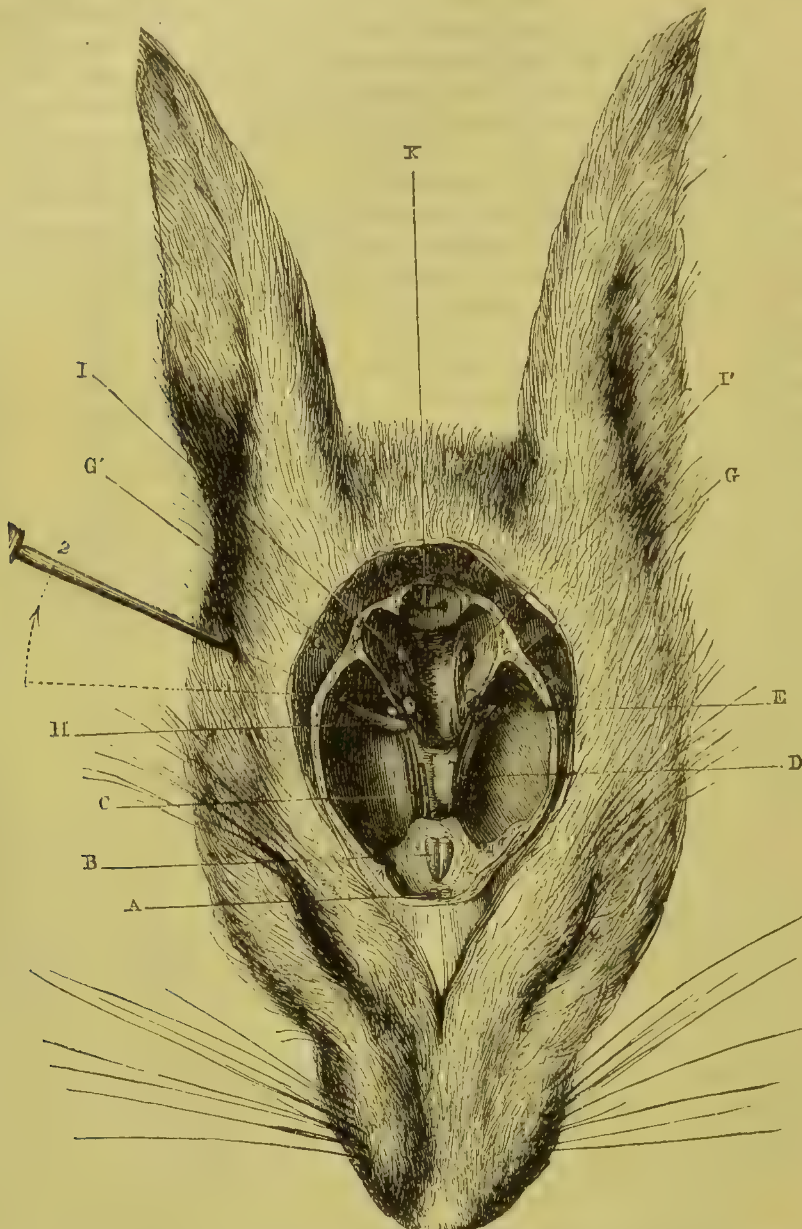


Fig. 217.—*Operation for division of the fifth nerve.* (Bernard.)
The calvarium and the cerebrum are removed in order to show the roots of the nerves and the direction of the instrument used in section of the fifth. A, olfactory nerves; B, optic nerves; C, motores oculorum communes; D, pathetici; E, fifth nerve; H, *blade of the instrument in the cranial cavity*; G, G′ I, I′, seventh pair of nerves; K, section of the spinal cord.

Immediate Effects of Division of the Trifacial.—It is hardly necessary to discuss the effects which instantly follow upon its division, after the statement of the functions of the trifacial, taken in connection with its physiological anatomy. The nerve has never been exposed in the cranial cavity in living animals; but its branches upon the face and the lingual branch of the inferior maxillary division have been operated upon and found to be exquisitely sensitive. Longet and others have exposed the roots in animals immediately after death, and have found that galvanization of the large root carefully insulated produces no muscular contraction. All who have divided this root in living animals must have recognized, not only that it is sensitive, but that its sensibility is far more acute than that of any other nervous trunk in the body. It is much more satisfactory to divide the nerve without etherizing the animal, as the evidence of pain is an important guide in this delicate operation; but, in using anæsthetics, we have never been able to bring an animal under their influence so completely as to abolish the sensibility of the root itself. For example, in cats that appear to be thoroughly etherized, as soon as the instrument touches the nerve, there is more or less struggling. The large root of the fifth, then, is an exclusively sensory nerve, and its sensibility is more acute than that of any other of the cerebro-spinal nerves.

As far as audition and olfaction are concerned, there are no special effects immediately following section of the trifacial; but there are interesting phenomena observed in connection with the eye and the organs of taste.

At the instant of division of the fifth, by the method just described, the eyeball is protruded and the pupil becomes strongly contracted. This occurs in rabbits, and the contraction of the pupil was observed in the first operations of Magendie. The pupil, however, is usually restored to the normal condition in a few hours. Longet states that the pupil is dilated by division of the fifth in dogs and cats. After division of the nerve, the lachrymal secretion becomes very much less in quantity; but this is not the cause of the subsequent inflammation, for the eyes are not inflamed, as was shown by Magendie, even after extirpation of both lachrymal glands. The movements of the eyeball are not affected by division of the fifth.

Another of the immediate effects of complete division of the fifth nerve is loss of general sensibility in the tongue. Most experiments upon the influence of this nerve over the general sensibility and the sense of taste in the tongue have been made by dividing the lingual branch of the inferior maxillary division. When this branch is irritated, there are evidences of intense pain. When it is divided, the general sensibility and the sense of taste are destroyed in the anterior third or half of the tongue. It will be remembered, however, that the chorda tympani joins the lingual branch of the fifth as it passes between the pterygoid muscles, and that section of this branch of the facial abolishes the sense of taste in the anterior third or half of the tongue. If the gustatory properties of the lingual branch of the fifth be derived from the chorda tympani, lesions of the fifth not involving this nerve would be followed by loss of general sensibility, but the taste would be unaffected. This has been shown to be the fact, by cases of paralysis of general sensibility of the tongue without loss of taste in the human subject, which will be discussed more fully in connection with gustation.

Among the immediate effects of section of the fifth, is an interference with the reflex phenomena of deglutition. In some recent researches upon the action of the sensitive nerves in deglutition, by Waller and Prevost, it was found that, after section of the fifth upon both sides, it was impossible to excite movements of deglutition by stimulating the mucous membrane of the velum palati. After section of the superior laryngeal branches of the pneumogastrics, no movements of deglutition followed stimulation of the mucous membrane of the top of the larynx. In these experiments, when the fifth was divided upon one side, stimulation of the velum upon the corresponding side had no effect, while movements of deglutition were produced by irritating the velum upon the sound side. These experiments show that the fifth nerve is important in the reflex phenomena of deglutition, as a sensory nerve, conveying the impression from the velum palati to the nerve-centres. This action probably takes place through filaments which pass from the fifth to the mucous membrane through Meckel's ganglion.

Remote Effects of Division of the Trifacial.—After the ordinary operation of dividing the fifth nerve in the cranial cavity, the immediate loss of sensibility of the integument and mucous membranes of the face and head is usually supplemented by serious disturbances in the nutrition of the eye, the ear, and the mucous membranes of the nose and mouth. At a period varying from a few hours to one or two days after the operation, the eye upon the affected side becomes the seat of purulent inflammation, the cornea becomes opaque and ulcerates, the humors are discharged, and the organ is destroyed. Congestion of the parts is usually very prominent a few hours after division of the nerve. At the same time, there is an increased discharge from the mucous membranes of the nose and mouth upon the affected side, and ulcers appear upon the tongue and lips. It is probable, also, that disorders in the nutrition of the auditory apparatus follow the operation, although these are not so prominent. Animals affected in this way usually die in from fifteen to twenty days.

One of the most interesting facts, particularly in view of the information derived from later observations, in connection with the early experiments of Magendie, is, that he noted that "the alterations in nutrition are much less marked" when the division is effected behind the ganglion of Gasser, than when it is done in the ordinary way through the ganglion. It is difficult enough to divide the nerve completely within the cranium, and is almost impossible to make the operation at will through or behind the ganglion; and the phenomena of inflammation are absent only in exceptional and accidental instances. Magendie offers no satisfactory explanation of the differences in the consecutive phenomena coincident with the locality of section of the nerve. The facts, however, have been abundantly verified. In the numerous experiments that we have made upon the fifth pair, we have generally noted the consecutive inflammatory phenomena in the order above described; but, in exceptional instances, these phenomena have been wanting. The following experiment illustrates these exceptional operations:

February 6, 1868, the fifth pair of nerves was divided upon the left side in a full-grown rabbit in the ordinary way, before the class at the Bellevue Hospital Medical College. There followed instant and complete loss of sensibility upon the left side of the face. Four days after, the animal having been fed *ad libitum* with cabbage, the loss of sensibility was still complete. There was very little redness of the conjunctiva of the left eye, and a very slight streak of opacity, so slight that it was distinguished with difficulty. Twelve days after the operation, the sensibility of the left eye was distinct but slight. There was no redness of the conjunctiva, and the opacity of the cornea had disappeared. The animal was in good condition, and the line of contact of the upper with the lower incisors, when the jaws were closed, was very oblique. The animal was kept alive by careful feeding with bread and milk for one hundred and seven days after the operation, there never being any inflammation of the organs of special sense. It died at that time of inanition, having become very much emaciated. The animal never recovered power over the muscles of mastication of the left side, and the incisors grew to a great length, interfering very much with mastication, which seemed to be the cause of death.

Longet, in 1842, furnished a satisfactory explanation of the absence of inflammation in certain cases of division of the fifth. He attributed the consecutive inflammation in most experiments to lesion of the ganglion of Gasser and of the sympathetic connections, which are very numerous at this point. These sympathetic filaments are avoided when the section is made behind the ganglion.

The explanation of the phenomena of disordered nutrition in the organs of special sense, particularly the eye, following division of the fifth, is not afforded by the section of this nerve alone; for, as we have seen, when the loss of sensibility is complete after division of the nerve behind the Gasserian ganglion, these results may not follow. Nor are they explained by deficiency in the lachrymal secretion, for they are not observed when both lachrymal glands have been extirpated. They are not due to exposure of the eyeball, for they do not follow upon section of the facial. Nor are they due simply to an enfeebled general condition, for, in the experiment we have detailed, the animal died of inanition after section of the nerve, without any evidences of inflammation. In view of the fact that section of the sympathetic filaments is well known to modify the nutrition of parts to which they are distributed, producing congestion, increase in temperature, and other phenomena, it is rational to infer that the modifications in nutrition which follow section of the fifth after it receives filaments from the sympathetic system, not occurring when these sympathetic filaments escape division, are to be attributed to lesion of the sympathetic, and not to the division of the sensory nerve itself.

A farther explanation is demanded for the inflammatory results which follow division of the sympathetic filaments joining the fifth, inasmuch as division of the sympathetic alone in the neck produces simply exaggeration of the nutritive processes, as evidenced chiefly by local increase in the animal temperature, and not the well-known phenomena of inflammation.

It has been remarked by Bernard, that the "alterations in nutrition appear more promptly in animals that are enfeebled." Section of the small root of the fifth, which is unavoidable when the nerve is divided within the cranial cavity, generally interferes so much with mastication as to influence seriously the general nutrition; and this might modify the nutritive processes in delicate organs, like the eye, so as to induce those changes which are called inflammatory. The following observation, communicated by Dr. W. H. Mason, Professor of Physiology in the Medical Department of the University of Buffalo, is very striking in this connection:

The fifth pair of nerves was divided in a cat in the ordinary way. By feeding the animal carefully with milk and finely-chopped meat, the nutrition was maintained at a high standard, and no inflammation of the eye occurred for about four weeks. The supply of food was then diminished to about the quantity it would be able to take without any special care, when the eye became inflamed, and perforation of the cornea and destruction of the organ followed. The animal was kept for about five months; at the end of which time, sensation upon the affected side, which had been gradually improving, was completely restored.

The explanation we have to offer of the consecutive inflammatory effects of section of the fifth with its communicating sympathetic filaments is the following: By dividing the sympathetic, the eye and the mucous membranes of the nose, mouth, and ear are rendered hyperæmic, the temperature is probably raised, and the processes of nutrition are exaggerated. This condition of the parts would seem to require a full supply of nutritive material from the blood, in order to maintain the condition of exaggerated nutrition; but, when the blood is impoverished—probably as the result of deficiency in the introduction of nutritive matter, from paralysis of the muscles of mastication upon one side—the nutritive processes in these delicate parts are seriously modified, so as to constitute inflammation. The observation just detailed is an argument in favor of this view; for here the inflammatory action seemed to be arrested when the action of the paralyzed muscles was supplied by careful feeding. With this view, the disorders of nutrition observed after division of the fifth may properly be referred to the sympathetic system.

Pathological facts in confirmation of experiments upon the fifth pair in the lower animals are not wanting; but it must be remembered that, in cases of paralysis of the nerve in the human subject, it is not always possible to locate exactly the seat of the lesion and to appreciate fully its extent, as can be done when the nerve is divided by an operation. In studying these cases, it sometimes occurs that the phenomena, particularly those of modified nutrition, are more or less contradictory.

In nearly all works upon physiology, we find references to cases of paralysis of the fifth in the human subject. In a recent article by Dr. H. D. Noyes, Professor of Ophthalmology in the Bellevue Hospital Medical College, two interesting cases are reported, which we had an opportunity of examining during the progress of treatment. In both of these cases there was inflammation of the eye. In one case, the tongue was entirely insensible upon one side, but there was no impairment of the sense of taste. An interesting feature in one of the cases was the fact that an operation upon the eyelid of the affected side was performed without the slightest evidence of pain on the part of the patient.

Cases of paralysis of the fifth in the human subject in the main confirm the results of experiments upon the inferior animals. In all the cases in which the fifth nerve alone was involved in the disease, without the portio dura of the seventh, there was simply loss of sensibility upon one side, the movements of the superficial muscles of the face being unaffected. When the small root was involved, the muscles of mastication upon one side were paralyzed; but, in certain cases in which this root escaped, there was no muscular paralysis. The senses of sight, hearing, and smell, except as they were affected by consecutive inflammation, were little if at all disturbed in uncomplicated cases. The sense of taste in the anterior portion of the tongue was perfect, except in those cases in which the seventh, the chorda tympani, or the lingual branch of the fifth after it had been joined by the chorda tympani, was involved in the disease. In some cases, there was no alteration in the nutrition of the organs of special sense; but in this respect the facts with regard to the seat of the lesion are not so satisfactory as in experiments upon the lower animals, it being difficult, in most of them, to limit the exact boundaries of the lesion.

Pneumogastric, or Par Vagum Nerve. (*Second Division of the Eighth Nerve.*)

Of all the nerves emerging from the cranial cavity, the pneumogastric, the second division of the eighth pair, presents the greatest number of anastomoses, the most remarkable course, and the most varied and interesting functions. Arising from the medulla oblongata by a purely sensory root, it communicates with at least five motor nerves in its course, and it is distributed largely to muscular tissue, both of the voluntary and the involuntary variety. Finally, there is no nerve that has been the subject of such extended and elaborate anatomical and physiological investigations, and none, concerning the properties and exact functions of which there has been so much difference of opinion.

We shall have to treat of the influence of the pneumogastric upon the act of deglutition, the heart and circulatory system, the respiratory system, the stomach, the intestines, and various glandular organs. An indispensable introduction to this study is a description of its physiological anatomy.

Physiological Anatomy of the Pneumogastric Nerve.—The apparent origin of the pneumogastric is from the lateral portion of the medulla oblongata, just behind the olivary body, between the roots of the glosso-pharyngeal and of the spinal accessory. The deep origin is mainly from what is sometimes called the nucleus of the pneumogastric, in the inferior portion of the gray substance in the floor of the fourth ventricle. The course of the fibres, traced from without inward, is somewhat intricate.

The deep origins of the pneumogastric and glosso-pharyngeal nerves appear to be, in the main, identical. Tracing the filaments from without inward, they may be followed in four directions. The anterior filaments pass from without inward, first very superficially and directed toward the olivary body, but, turning before they reach the olivary body, they pass deeply into the substance of the restiform body, in which they are lost. The posterior filaments are superficial, and they pass, with the fibres of the restiform body, toward the cerebellum. Of the intermediate filaments, the anterior pass through the restiform body, the greatest number extending to the median line in the floor of the fourth ventricle. A few fibres are lost in the middle fasciculi of the medulla, and a few pass toward the brain. The posterior intermediate filaments traverse the restiform body to the floor of the fourth ventricle, when some pass to the median line, and others descend in the substance of the medulla. It is difficult to follow the fibres of origin of the pneumogastrics beyond the median line; but recent observations leave no doubt of the fact that many of these fibres decussate in the floor of the fourth ventricle.

There are two ganglionic enlargements belonging to the pneumogastric. In the jugular foramen, is a well-marked, grayish, ovoid enlargement, from one-sixth to one-fourth of an inch in length, called the jugular ganglion, or the ganglion of the root. This is united by two or three filaments with the ganglion of the glosso-pharyngeal. It is a true ganglion, containing nerve-cells. After the nerve has emerged from the cranial cavity, it presents on its trunk another grayish enlargement, from half an inch to an inch in length, called the ganglion of the trunk. This is of rather a plexiform structure, the white fibres being mixed with grayish fibres and nerve-cells. The exit of the nerve from the cranial cavity is by the jugular foramen, or posterior foramen lacerum, in company with the spinal accessory, the glosso-pharyngeal, and the internal jugular vein.

FIG 218.—*Anastomoses of the pneumogastric.* (Hirschfeld.)

1. facial nerve; 2, glosso-pharyngeal nerve; 2′, anastomoses of the glosso-pharyngeal with the facial; 3, 3, *pneumogastric, with its two ganglia;* 4, 4, *spinal accessory;* 5. sublingual nerve; 6, superior cervical ganglion of the sympathetic; 7, *anastomosic arcade of the first two cervical nerves;* 8, carotid branch of the superior cervical ganglion of the sympathetic; 9, nerve of Jacobson; 10, branches of this nerve to the sympathetic; 11, branch to the Eustachian tube; 12, branch to the fenestra ovalis; 13, branch to the fenestra rotunda; 14, external deep petrous nerve; 15, internal deep petrous nerve; 16, otic ganglion; 17, *auricular branch of the pneumogastric;* 18, *anastomosis of the pneumogastric with the spinal accessory;* 19, *anastomosis of the pneumogastric with the sublingual;* 20, anastomosis of the spinal accessory with the second pair of cervical nerves; 21, pharyngeal plexus; 22, superior laryngeal nerve.

Anastomoses.—The filaments of communication which the pneumogastric receives from other nerves are interesting from their great importance and their varied sources. The most important of these is the branch from the spinal accessory. There are occasional filaments of communication which pass from the spinal accessory to the ganglion of the root, but these are not constant. After both nerves have emerged from the cranial cavity, an important branch of considerable size passes from the spinal accessory to the pneumogastric, with which it becomes closely united. Experiments have shown that these filaments from the spinal accessory pass in great part to the larynx by the inferior laryngeal nerves.

In the aquæductus Fallopii, the facial nerve gives off a filament of communication to the pneumogastric at the ganglion of the root. This filament, joined at the ganglion by sensory filaments from the pneumogastric and some filaments from the glosso-pharyngeal, is called the auricular branch of Arnold. By some anatomists it is regarded as a branch from the facial, and by others it is described with the pneumogastric.

Two or three small filaments of communication pass from the sublingual to the ganglion of the trunk of the pneumogastric.

At the ganglion of the trunk, the pneumogastric generally receives filaments of communication from the arcade formed by the anterior branches of the first two cervical nerves. These, however, are not constant.

The pneumogastric is connected with the sympathetic system by numerous delicate filaments of communication received from the superior cervical ganglion, passing in part upward toward the ganglion of the root of the pneumogastric, and in part transversely and downward. These filaments are frequently short, and they bind, as it were, the sympathetic ganglion to the trunk of the nerve. The main trunk of the pneumogastric and its branches receive a few delicate filaments of communication from the middle and inferior cervical and the upper dorsal ganglia of the sympathetic.

The pneumogastric frequently sends a very delicate filament to the glosso-pharyngeal nerve, at or near the ganglion of Andersch. Branches from the pneumogastric join branches from the glosso-pharyngeal, the spinal accessory, and the sympathetic, to form the pharyngeal plexus.

Distribution.—In describing the very extensive distribution of the pneumogastrics, while the nerves upon the two sides do not present any important differences in the destination of their filaments as far down as the diaphragm, it will be seen that the abdominal branches are not the same. The most important branches are the following:

1. Auricular.
2. Pharyngeal.
3. Superior laryngeal.
4. Inferior, or recurrent laryngeal.
5. Cardiac, cervical and thoracic.
6. Pulmonary, anterior and posterior.
7. Œsophageal.
8. Abdominal.

FIG. 219.—*Distribution of the pneumogastric.* (Hirschfeld.)
1, *trunk of the left pneumogastric*; 2, *ganglion of the trunk*; 3, *anastomosis with the spinal accessory*; 4, *anastomosis with the sublingual*; 5, *pharyngeal branch (the auricular branch is not shown in the figure)*; 6, *superior laryngeal branch*; 7, *external laryngeal nerve*; 8, *laryngeal plexus*; 9, 9, *inferior laryngeal branch*; 10, *cervical cardiac branch*; 11, *thoracic cardiac branch*; 12, 13, *pulmonary branches*; 14, lingual branch of the fifth; 15, lower portion of the sublingual; 16, glosso-pharyngeal; 17, spinal accessory; 18, 19, 20, spinal nerves; 21, phrenic nerve; 22, 23, spinal nerves; 24, 25, 26, 27, 28, 29, 30, sympathetic ganglia.

The auricular nerves are sometimes described in connection with the facial. They are given off from the ganglion of the trunk of the pneumogastric, and are composed of filaments of communication from the facial and from the glosso-pharyngeal, as well as of filaments from the pneumogastric itself. The nerves thus constituted are distributed to the integument of the upper portion of the external auditory meatus, and a small filament is sent to the membrana tympani.

The pharyngeal nerves are very remarkable in their course. They are given off from the superior portion of the ganglion of the trunk and contain a large number of the filaments of communication which the pneumogastric receives from the spinal accessory. In their course by the sides of the superior constrictor muscles of the pharynx, these nerves anastomose with numerous filaments from the glosso-pharyngeal and the superior cervical ganglion of the sympathetic, to form what is known as the pharyngeal plexus. The ultimate filaments of distribution pass to the muscles and the mucous membrane of the pharynx. Physiological experiments have shown that the motor influence transmitted to the pharyngeal muscles through the pharyngeal branches of the pneumogastric is derived from the spinal accessory.

The superior laryngeal nerves are given off from the lower part of the ganglion of the trunk. Their filaments come from the side opposite to the point of junction of the pneumogastric with the communicating branch from the spinal accessory, so that probably the superior laryngeals contain few if any motor fibres from this nerve. The superior laryngeal gives off the external laryngeal, a long, delicate branch, which sends a few filaments to the inferior constrictor of the pharynx and is distributed to the crico-thyroid muscle and the mucous membrane of the ventricle of the larynx. The external laryngeal anastomoses with the inferior laryngeal and with the sympathetic. The internal branch is distributed to the mucous membrane of the epiglottis, the base of the tongue, the aryteno-epiglottidean fold, and the mucous membrane of the larynx as far down as the true vocal cords. A branch from this nerve, in its course to the larynx, penetrates the arytenoid muscle, to which it sends a few filaments, but these are all sensory. This branch also supplies the crico-thyroid muscle. It anastomoses with the inferior laryngeal nerve. An important branch, described by Cyon and Ludwig, in the rabbit, under the name of the depressor-nerve, arises by two roots, one from the superior laryngeal and the other from the trunk of the pneumogastric, passes down the neck by the side of the sympathetic, and, in the chest, joins filaments from the thoracic sympathetic, to penetrate the heart between the aorta and the pulmonary artery. This nerve will be referred to more particularly in connection with the influence of the pneumogastrics upon the circulation.

It is important, from a physiological point of view, to note that the superior laryngeal nerve is the nerve of sensibility of the upper part of the larynx, as well as of the supra-laryngeal mucous membranes, and that it animates a single muscle of the larynx (the crico-thyroid) and the inferior constrictor of the pharynx.

The inferior, or recurrent laryngeal nerves present some slight differences in their anatomy upon the two sides. Upon the left side, the nerve is the larger and is given off at the arch of the aorta. Passing beneath this vessel, it ascends in the groove between the trachea and the œsophagus. In its upward course, it gives off certain filaments which join the cardiac branches, filaments to the muscular tissue and mucous membrane of the upper part of the œsophagus, filaments to the mucous membrane and the inter-cartilaginous muscular tissue of the trachea, one or two filaments to the inferior constrictor of the pharynx, and a branch which joins the superior laryngeal. Its terminal branches penetrate the larynx, behind the posterior articulation of the thyroid with the cricoid cartilage, and are distributed to all of the intrinsic muscles of the larynx, except the crico-thyroids, which are supplied by the superior laryngeal. Upon the right side, the nerve winds from before backward around the subclavian artery, and it has essentially the same course and distribution as upon the left side, except that it is smaller and its filaments of distribution are not so numerous.

The important physiological point connected with the anatomy of the recurrent laryngeals is that they animate all of the intrinsic muscles of the larynx, except the crico-thyroid. Experiments have shown that these nerves contain numerous filaments from the spinal accessory.

The cervical cardiac branches, two or three in number, arise from the pneumogastrics at different points in the cervical portion and pass to the cardiac plexus, which is formed in great part of filaments from the sympathetic. The thoracic cardiac branches are given off from the pneumogastrics below the origin of the inferior laryngeals and join the cardiac plexus.

The anterior pulmonary branches are few and delicate as compared with the posterior branches. They are given off below the origin of the thoracic cardiac branches, send a few filaments to the trachea, and then form a plexus which surrounds the bronchial tubes and follows the bronchial tree to its terminations in the air-cells. The posterior pulmonary branches are larger and more numerous than the anterior. They communicate freely with sympathetic filaments from the upper three or four thoracic ganglia and then form the great posterior pulmonary plexus. From this plexus, a few filaments go to the inferior and posterior portion of the trachea, a few pass to the muscular tissue and mucous membrane of the middle portion of the œsophagus, and a few are sent to the posterior and superior portion of the pericardium. The plexus then surrounds the bronchial tree and passes with its ramifications to the pulmonary tissue, like the corresponding filaments of the anterior branches. The pulmonary branches are distributed to the mucous membrane, and not to the walls of the blood-vessels.

The œsophageal branches take their origin from the pneumogastrics above and below the pulmonary branches. These branches from the two sides join to form the œsophageal plexus, their filaments of distribution going to the muscular tissue and the mucous membrane of the lower third of the œsophagus.

The abdominal branches are quite different in their distribution upon the two sides.

Upon the left side, the nerve, which is situated anterior to the cardiac opening of the stomach, immediately after its passage by the side of the œsophagus into the abdomen, divides into numerous branches, which are distributed to the muscular walls and the mucous membrane of the stomach. As the branches pass from the lesser curvature, they take a downward direction and go to the liver, and, with another branch running between the folds of the gastro-hepatic omentum, they follow the course of the portal vein in the hepatic substance. The branches of this nerve anastomose with the nerve of the right side and with the sympathetic.

The right pneumogastric, situated posteriorly, at the œsophageal opening of the diaphragm, sends a few filaments to the muscular coat and the mucous membrane of the stomach, passes backward, and is distributed to the liver, spleen, kidneys, suprarenal capsules, and finally to the whole of the small intestine. The branches to the small intestine are very important. These were accurately described in 1860, by Kollmann, in an elaborate and beautifully-illustrated prize-essay. In the plate showing the distribution of this nerve, it is seen that the branches to the intestine are very numerous. According to these researches, the branches described belong to the pneumogastric itself and are not derived from the sympathetic. When we come to treat of the action of the pneumogastric upon the small intestine, it will be seen that the anatomical researches by Kollmann have been fully confirmed by physiological experiments. Before the nerves pass to the intestines, there is a free anastomosis and interchange of filaments between the right and the left pneumogastric.

Properties and Functions of the Pneumogastric Nerves.

There is no nerve in the body that has been the subject of so many experiments, and concerning which so much has been written, as the pneumogastric. Its accessible position in many parts of its course, its extensive connections with the digestive, the respiratory, and the circulatory system, and the evident importance of its relations, have rendered the literature connected with its physiology somewhat redundant. We do not propose to discuss in full all of the views entertained from time to time with regard to its functions, but shall state merely what seem to be well-ascertained facts, and the most reasonable inferences, where the facts are difficult of demonstration. In treating of the functions of this nerve, we shall be compelled to make constant reference to its anatomy, and for that reason we have described pretty fully in detail most of the important points in its connections and distribution.

Although the extensive distribution of the pneumogastrics and their importance will necessitate a long discussion of their physiology, we shall endeavor to separate the points to be considered distinctly, and to simplify the subject as much as possible.

We shall first treat of the general properties of those filaments derived from the true roots of the nerves, and, following them in their course, shall note the properties derived from their connections with other nerves.

We shall then treat of the properties of the different branches of the nerves, under distinct heads, taking up these branches as they are given off, from above downward. In this, we shall consider first the properties and functions of the auricular branches; next, the pharyngeal branches, with their influence upon the action of the pharynx in deglutition; next, the superior and inferior laryngeal branches, with their relations to the physiology of the larynx; next, the cardiac branches, with their influence on the movements of the heart and the circulation; next, the pulmonary branches, with the function of the nerves in connection with respiration; next, the œsophageal branches, in connection with the influence of the nerves upon the action of the œsophagus, in deglutition; and finally, the abdominal branches, with the influence of the nerves upon digestion and the functions of the abdominal viscera. By dividing up, in this way, the action of the pneumogastrics, it is hoped that their physiology may be relieved of much of the complexity in which it is apparently involved.

General Properties of the Roots of Origin of the Pneumogastrics.—All who have operated upon the pneumogastrics in the cervical region in living animals have noted their exceedingly dull sensibility as compared with the ordinary sensory nerves. Bernard, indeed, states that in this region they are generally insensible; but we have usually found, in dogs at least, that their division is attended with slight evidences of pain. Without citing in detail all the experiments upon this point, it is sufficient to state that some physiologists, on galvanizing or otherwise irritating the roots of the nerves in animals just killed, have noted movements of the muscles of deglutition, of the œsophagus, and of the muscular coats of the stomach. These experiments have led to the opinion that the proper roots of the nerves are motor as well as sensory. It becomes, therefore, a difficult as well as an important point to determine whether or not the roots be of themselves exclusively sensory or mixed. In discussing the properties of the roots, we shall rely almost entirely upon direct experiments; although the arguments drawn from their anatomical characters, in the presence of ganglia and the deep origin of their fibres, point strongly to their sensory character. It is impossible to stimulate the roots, before they have received motor filaments from other nerves, in living animals, and the experiments are therefore made upon animals just killed, before the nervous irritability has disappeared. If the true roots of the nerves be exclusively sensory, their galvanization in animals just killed should produce, by direct action, no muscular contraction. If the roots contain any motor filaments, contraction of muscles should follow their stimulation. The proper physiological conditions in such experiments are the following:

1. It is necessary to stimulate the roots so that the filaments from the spinal accessory and from other motor nerves are not involved.

2. It is important to ascertain, provided movements follow such irritation, whether or not they be due to reflex action.

The first of these conditions is easily fulfilled. All that is necessary is to stimulate the roots before the nerves have received any anastomosing filaments. To avoid contractions of muscles due to reflex action, it is best to divide the roots and to stimulate their distal portion. If it be true that stimulation of the distal extremities of the roots—the irritation so applied as not to involve communicating filaments from motor nerves, and not to be conveyed to the centres, producing reflex movements through other nerves—does not produce any movements, it is fair to assume that the true filaments of origin are exclusively sensory. The facts upon this point demand careful and critical study; and it will be proper to discard the earlier experiments, made before the mechanism of reflex action had been satisfactorily established.

If the experiments of Longet be accepted without reserve, they prove—as conclusively as is possible without exposing the roots in living animals, an operation which is impracticable—that the true filaments of origin of the pneumogastrics are exclusively sensory, or, at least, that the nerve contains no motor filaments except those derived from other nerves. The following quotation gives the essential points in these experiments:

"In dogs of large size and in horses, I have isolated in the cranium, with the most minute care, the pneumogastric of the medulla oblongata and the superior filaments of the spinal accessory (*internal branch*), in order to avoid all *reflex movement* and any derivative current upon the last-named nerve; I then immediately caused the current to act exclusively upon the filaments of origin of the pneumogastric, without having ever seen the slightest contraction supervene, either in the muscles of the larynx or pharynx, or in the muscular tunic of the œsophagus, or elsewhere.

"But also I have never failed to demonstrate to all those who witnessed my experiments, how it is easy to obtain opposite results in neglecting only one precaution: it suffices, for example, to slightly moisten the slip of glass or oiled silk which serves to isolate the two nerves, in order that the current should act immediately upon the superior filaments of the spinal accessory, from which we have marked contractions in the organs just mentioned."

These experiments seem entirely conclusive. In treating of the reflex phenomena of deglutition and their relations to the superior branches of the pneumogastric, the pharyngeal, and the superior laryngeal, it will be seen that irritation, either of these nerves or of the mucous membranes to which they are distributed, will produce contractions in the muscles. All who are practically familiar with the application of electricity to the nerves know how difficult it is to insulate the nervous trunks so as to avoid the influence of "derived" currents. In carefully studying the experiments of Longet, it seems that all the physiological conditions were fulfilled; and that, when the nerve is divided at the root and the stimulation is applied to the peripheral end, so as to cut off all reflex action from the nervous centres, and when sufficient care is exercised to prevent the propagation of the current to the motor connections of the pneumogastric, the nerve, from its origin at the medulla oblongata to the ganglion of the root, contains no motor filaments and is exclusively sensory. We shall therefore adopt, without reserve, the conclusions of Longet, that the true filaments of origin of the pneumogastrics are exclusively sensory, or, at least, that they have no motor properties.

Properties and Functions of the Auricular Nerves.—There is very little to be said with regard to the auricular nerves, after the description we have given of their anatomy. They are sometimes described with the facial and sometimes with the pneumogastric. They contain filaments from the facial, the pneumogastric, and the glosso-pharyngeal. The sensory filaments of these nerves give sensibility to the upper part of the external auditory meatus and the membrana tympani.

Properties and Functions of the Pharyngeal Nerves.—The pharyngeal branches of the pneumogastric are mixed nerves, their motor filaments being derived from the spinal accessory. Their direct action upon the muscles of deglutition belongs to the physiological history of the last-named nerve. We have already stated, in treating of the spinal accessory, that the filaments of communication that go to the pharyngeal branches of the pneumogastric are distributed to the pharyngeal muscles.

It is impossible to divide all of the pharyngeal filaments in living animals and observe directly how far the general sensibility of the pharynx and the reflex phenomena of deglutition are influenced by this section. As far as we can judge from the distribution of the filaments to the mucous membrane, it would seem that they combine with the pharyngeal filaments of the fifth, and possibly with sensory filaments from the glosso-pharyngeal, in giving general sensibility to these parts.

In some recent experiments by Waller and Prevost, upon the reflex phenomena of deglutition, it is shown that the action of the pharyngeal muscles cannot be excited by stimulation of the mucous membrane of the supra-laryngeal region and the pharynx, after section of the fifth and of the superior laryngeal branch of the pneumogastric. This would seem to show that the pharyngeal branches of the pneumogastrics are of little or no importance in these reflex phenomena.

Properties and Functions of the Superior Laryngeal Nerves.—The distribution of these nerves points to a double function; viz., an action upon the crico-thyroid muscles, and the important office of supplying general sensibility to the upper part of the larynx and a portion of the surrounding mucous membrane. The stimulation of these nerves produces intense pain and contraction of the crico-thyroids; but it has been shown by experiment that the arytenoid muscles, through which the nerves pass, receive no motor filaments. The action of the nerves upon the muscles is very simple, and resolves itself into the function of the crico-thyroids, which has been treated of fully under the head of phonation. When these muscles are paralyzed, the voice becomes hoarse. The filaments to the inferior muscles of the pharynx are few and comparatively unimportant. It is important in this connection to note that the superior laryngeals do not receive their motor filaments from the spinal accessory.

The sensory filaments of the superior laryngeals have important functions connected with the protection of the air-passages from the entrance of foreign matters, particularly in deglutition, and are farther concerned, as we shall see, in the reflex action of the constrictors of the pharynx. In treating of deglutition, we have fully discussed the importance of the exquisite sensibility of the top of the larynx in the protection of the air-passages. When both superior laryngeals have been divided in living animals, liquids often pass into the larynx in small quantity, owing to the absence of the reflex closure of the glottis when foreign matters are brought in contact with its superior surface, and the occasional occurrence of inspiration during deglutition.

Aside from the protection of the air-passages, the superior laryngeal is one of the sensory nerves through which the reflex acts in deglutition operate. There are certain parts which depend for their sensibility entirely upon this nerve; viz., the mucous membrane of the epiglottis, the aryteno-epiglottidean fold, and the larynx as far down as the true vocal cords. When an impression is made upon these parts, as when they are touched with a piece of meat, regular and natural movements of deglutition ensue.

The experiments made by galvanizing the trunks of the superior laryngeal nerves are extremely interesting. If the nerves be divided and galvanization be applied to their central ends, movements of deglutition are observed, and there is also arrest of the action of the diaphragm. From these experiments, it would seem that the impression which gives rise to the movements of deglutition aids in protecting the air-passages from the entrance of foreign matters, by temporarily arresting the inspiratory act.

An important point for our consideration, in this connection, is the action of the superior laryngeal nerves in the ordinary phenomena of deglutition; and, in experiments with galvanism, a feeble current simulates most nearly the natural processes. In such experiments the results have been quite satisfactory. The experiments in which a powerful current of galvanism has been applied to the nerves also show an arrest of respiration; but it is argued that there is nothing special in the action of the superior laryngeals under these conditions, inasmuch as other sensitive nerves have been found to act in the same way. This is undoubtedly true; but it is well known that, in living animals, strong impressions made upon any of the acutely sensitive nerves arrest respiration, and that this is one of the phenomena commonly observed in animals struggling under painful operations. In view of these facts, it seems unnecessary to discuss more fully the numerous experiments with regard to the effects upon respiration of stimulation of the superior laryngeals; and we can assume that it has been demonstrated that an impression made upon the terminal filaments of these nerves, such as occurs in the ordinary process of deglutition, excites, by reflex action, contraction of the constrictors of the pharynx, and, at the same time, momentarily suspends the movements of the diaphragm.

Important experiments have been made within the past few years, upon the action of the pneumogastrics on the circulation, in which it is claimed that nervous filaments, arising, in the rabbit, in part from the trunk of the pneumogastric and in part from the superior laryngeal branch, act as reflex depressors of the vascular tension. These experiments will be fully discussed in connection with the cardiac branches.

Properties and Functions of the Inferior, or Recurrent Laryngeal Nerves.—The anatomical distribution of these nerves shows that their most important function is connected with the muscles of the larynx. The few filaments which are given off in the neck to join the cardiac branches are probably not very important. It is proper to note, however, that the inferior laryngeal nerves supply the muscular tissue and mucous membrane of the upper part of the œsophagus and the trachea, and one or two branches are sent to the inferior constrictor of the pharynx. The function of these filaments is sufficiently evident.

The inferior laryngeals contain chiefly motor filaments, judging from their distribution as well as from the effects of direct irritation. All who have experimented upon these nerves have noted little or no evidence of pain when they are stimulated or divided.

One of the most important functions of the recurrents is connected with the production of vocal sounds. We have already fully treated of the mechanism of the voice and the action of the intrinsic muscles of the larynx; and, in our account of the physiology of the internal, or communicating branch from the spinal accessory to the pneumogastric, it has been shown that this is the true nerve of phonation. In the older works upon physiology, before the functions of the spinal accessory were fully understood, the experiments upon the inferior laryngeals led to the opinion that these were the nerves of phonation, as they showed loss of voice following their division in living animals. It is true that these nerves contain the filaments which preside over the vocal movements of the larynx; but it is also the fact that these vocal filaments are derived exclusively from the spinal accessory, and that the recurrents contain as well motor filaments which preside over movements of the larynx not concerned in the production of vocal sounds.

The muscles of the larynx concerned in phonation are, the crico-thyroids, animated by the superior laryngeals, and the arytenoid, the lateral crico-arytenoids, and the thyro-arytenoids, animated by the inferior laryngeals. The posterior crico-arytenoids are respiratory muscles; and it is curious that these are not affected by extirpation of the spinal accessories, but that the glottis is still capable of dilatation, so that inspiration is not impeded. If, however, the spinal accessories be extirpated, and the larynx be then exposed in a living animal, the glottis still remains dilated, but will not close when irritated. If the inferior laryngeals be then divided, the glottis is mechanically closed with the inspiratory act, and the animals often die of suffocation. When we call to mind the varied sources from which the pneumogastrics receive their motor filaments, it is easy to understand how certain of these may preside over the vocal movements, and others, from a different source, may animate the respiratory movements.

As we should naturally expect from what has already been said, section of the inferior laryngeal nerves paralyzes both the vocal and the respiratory movements of the larynx. It is not necessary to refer in detail to the ancient and modern experiments illustrating this point, the former dating from the time of Galen. In adult animals, the cartilages of the larynx are sufficiently rigid to allow of inspiration after the organ has been completely paralyzed; but, in young animals, the glottis is closed, and suffocation ensues. We have generally observed in cats, that suffocation follows immediately upon section of the recurrents or of the pneumogastrics in the neck.

The impediment to the entrance of air into the lungs is a sufficient explanation of the increase in the number of the respiratory acts after division of both recurrents. The acceleration of respiration is much greater in young than in adult animals. This does not apply to very young animals, in which section of the recurrents produces almost instant death.

Feeble galvanization of the central ends of the inferior laryngeals, after their division, produces rhythmical movements of deglutition, generally coincident with arrest of the action of the diaphragm. These phenomena are generally observed in rabbits, but they are not constant. The reflex action of these nerves in deglutition is probably dependent upon the communicating filaments which they send to the superior laryngeal nerves.

Properties and Functions of the Cardiac Nerves, and Influence of the Pneumogastrics upon the Circulation.—One of the most interesting questions connected with the physiology of the pneumogastric nerves is their action upon the heart; and the results of experiments, which will be fully detailed hereafter, are precisely the opposite of what would be expected in the case of a nerve containing motor filaments and distributed to a muscular organ. Section of the pneumogastrics in the neck, far from arresting the action of the heart, increases the rapidity of its pulsations; and galvanization of the nerves arrests the heart's action in diastole.

Within the past few years, some very remarkable experiments have been made upon the influence of certain nerves given off near the superior laryngeals, which have been called the depressors of the circulation; but most observations have been made upon the trunks of the pneumogastrics in the cervical region, as it is exceedingly difficult to isolate the thoracic cardiac branches and to operate upon them without involving other nervous filaments. In galvanizing the nerves in the neck, we have to consider both the direct influence of the current and the phenomena due to reflex action.

Effects of Section of the Pneumogastrics upon the Circulation.—It is not necessary to cite in detail the various experiments upon the effects of section of the pneumogastrics in the neck upon the action of the heart. The division of these nerves in living animals is sufficiently easy, and all who have performed this operation have noted the same results. By section of these nerves, the heart is at once separated from one of the most important of its nervous connections; and the effects show that, as far as this organ is concerned, the motor filaments present great differences from the ordinary motor nerves of the cerebro-spinal system. Most of the observations made by dividing the nerves have been upon dogs, and the differences in the effects upon other animals are slight and unimportant. The following are the important phenomena presented in typical experiments:

Section of one of the pneumogastrics in the neck does not produce any very marked effect upon the action of the heart, after the slight disturbance which usually follows the operation has passed away. The number of pulsations is slightly increased, and the cardiac pressure, as shown by a cardiometer fixed in the carotid artery, is slightly diminished; but this is insignificant as compared with the effects of dividing both nerves.

Section of both pneumogastrics usually produces immediate and serious disturbance in the respirations, which are momentarily accelerated. The animal usually becomes agitated and suffers from want of air; and, when it is desired especially to note the cardiac disturbance, it is often necessary to relieve the respiration by introducing a tube into the trachea. In full-grown dogs, however, the respirations soon become calm, but they are diminished in frequency and become unusually profound. When the animal is in this condition, the beats of the heart are very much increased in frequency, at least doubled; but they are inefficient and tremulous.

An interesting point in this connection is the want of influence of certain medicinal substances over the action of the heart in animals after division of the pneumogastrics. Traube has shown that, while digitalis injected into the veins of a dog was capable in an hour of reducing the pulse to about one-fourth of the normal number of beats per minute, there was no appreciable effect upon the circulation when the injection was made in animals with both pneumogastrics divided.

The influence of the pneumogastrics upon the heart is one of the most interesting points in the physiology of the circulation; but we can discuss the mechanism of the phenomena following section of the nerves more satisfactorily after we have considered the effects of their galvanization.

Effects of Galvanizing the Pneumogastrics or their Branches upon the Circulation.—The experiments upon the effects of galvanization of the pneumogastrics in the neck on the action of the heart are almost innumerable; and, although the explanations of the phenomena observed present the widest differences, the facts themselves are sufficiently simple. These facts will be discussed under the following heads: 1. The direct influence of galvanization of the nerves in the neck, undivided, or of galvanization of the peripheral extremities of the trunks after division. 2. Reflex phenomena following galvanization of the central ends of the pneumogastrics, after their division.

Fig. 220.—*Branches of the pneumogastric to the heart.* (Bernard.)
C, heart; *a*, carotid artery going to the brain; *u*, branches of the pneumogastric going to the heart.

Direct Influence of the Pneumogastrics upon the Heart.—In 1846, the brothers Weber noted the important fact, that galvanization of the pneumogastrics in the neck rendered the action of the heart slow, and, if the galvanization were sufficiently powerful, arrested the heart, which remained flaccid and in diastole for a certain time while the galvanization was continued. This fact has since been confirmed by numerous experimenters.

While there is no difference of opinion among physiologists with regard to the stoppage of the heart by powerful galvanization, it is stated by some that a very feeble current passed through the peripheral ends of the divided nerves quickens the heart's action; but it is admitted by all that it is very difficult to regulate the intensity of the current so as to produce this effect. After section of the nerves, the action of the heart is very readily modified by struggles, etc., on the part of the animal under observation; and, in view of the exceeding nicety of the reported experiments, it cannot be admitted that the heart is capable of being excited to increased rapidity of action, without observations of the most positive character. Such facts are wanting; and, farthermore, it has been shown by Dr. Rutherford, in a series of exceedingly exact and satisfactory experiments, that whenever a galvanic current passed through the pneumogastrics has any appreciable effect upon the action of the heart it is to diminish the frequency of its pulsations. Inasmuch as our object is simply to show that, imitating the nervous force by galvanism, the action of the pneumogastrics is inhibitory, we shall not discuss the effects of different currents, and other experiments, which have little relation to the natural action of the nerves, and possess slight interest from a purely physiological point of view.

The direct action of the pneumogastrics upon the heart is undoubtedly through their motor filaments. All the facts developed by experiments are in accordance with this view. If the nerves be divided in the neck, galvanization of the central ends has no effect upon the heart, the pulsations being arrested only when the peripheral ends are stimulated. This shows that, at least as far as the fibres passing down the neck are concerned, the action is centrifugal and direct, not reflex. Another curious fact illustrates the same point very forcibly. It is well known that the woorara-poison completely paralyzes the motor nerves, leaving the muscular irritability and the sensory nerves intact. It has been found that, in animals poisoned with woorara, the action of the heart being maintained by artificial respiration, galvanization of both pneumogastrics has no effect upon its pulsations. This fact we have repeatedly verified in public demonstrations. Still another curious fact remains bearing upon the question under consideration. If powerful galvanization, which immediately arrests the cardiac pulsations, be continued for a certain time, so that the motor filaments become temporarily exhausted and lose their irritability, the heart resumes its contractions, notwithstanding that the galvanization is continued; the nerves being for the time incapable of transmitting the inhibitory influence.

The source of the motor filaments in the pneumogastrics which exert a direct inhibitory action upon the heart becomes an important point to determine. In the original experiments by the brothers Weber, it was shown that, when the galvanic stimulus was applied to that portion of the centres from which the nerves take their origin, the action of the heart was arrested in the same way as when the nerves themselves are galvanized; and it has been shown by subsequent observations that, when the heart is thus arrested by galvanization of the medulla oblongata, if both pneumogastrics be divided in the neck, its action is resumed. This would at first lead to the supposition that the inhibitory filaments are derived from the roots themselves of the pneumogastrics; but it has been conclusively demonstrated that they are really derived from the spinal accessories, the upper filaments of origin of which are situated just below the roots of the pneumogastrics.

It has been shown that powerful galvanization of one pneumogastric will arrest the heart's action, and also that this inhibitory action is much more marked in the right than in the left nerve. Waller, after extirpating the spinal accessory nerve upon one side, found that galvanization of the pneumogastric upon that side had no effect upon the heart, provided that from ten to twelve days had elapsed after extirpation of the spinal accessory, a sufficient time to secure disorganization and loss of irritability of its fibres. These experiments show conclusively that the motor filaments contained in the pneumogastric, which act directly upon the heart, are derived exclusively from the communicating branch of the spinal accessory.

Reflex Influence, through the Pneumogastrics, upon the Circulation.—Galvanization of the central ends of the pneumogastrics, after their division in the neck, does not influence the action of the heart, except as the pulsations are affected by the modifications in respiration. When the central ends are stimulated, the pupils become dilated, the eyes protrude, sometimes vomiting occurs, and always the number of respiratory acts is diminished, and, with a powerful current, are arrested in inspiration; but the pulsations of the heart are not affected.

Depressor-Nerve.—An important reflex action operating upon the circulation through branches of the pneumogastrics has lately been described by Cyon and Ludwig, in a memoir which received the prize for Experimental Physiology from the French Academy of Sciences, in 1867. The experiments upon which this memoir is based are exceedingly

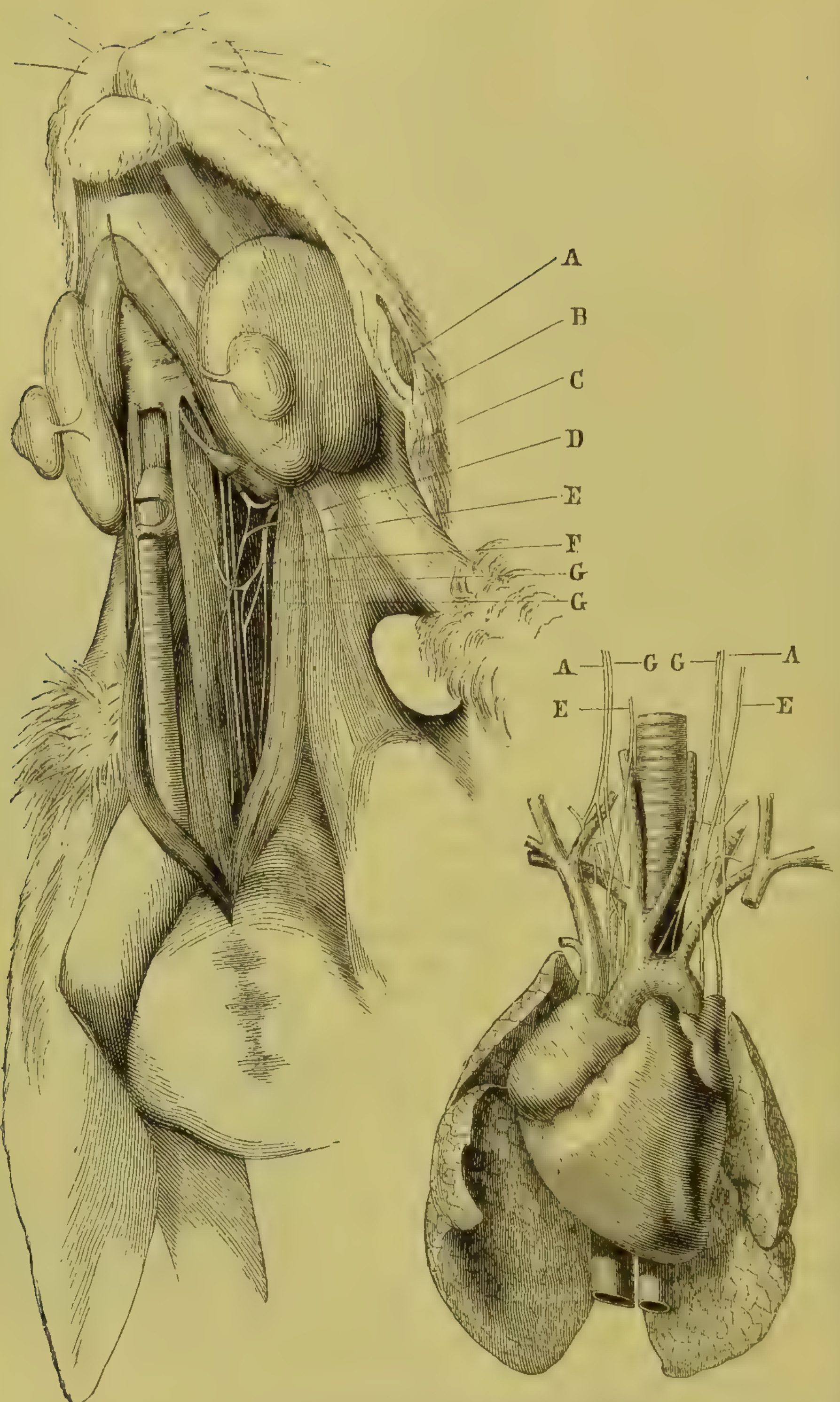


FIG. 221.—*Depressor-nerves.* (Cyon and Ludwig.)

A, A, A, sympathetic nerves; B, sublingual; C, descending branch of the sublingual; D, branch from the cervical plexus; E, E, E, pneumogastrics; F, superior laryngeal nerves; G, G, G, G, depressor-nerves.

clear and satisfactory, and they afford, perhaps, the only positive explanation we have of reflex action upon the heart. The substance of these observations is briefly as follows:

In the rabbit, is a nerve, arising by two roots, one coming from the trunk of the pneumogastric and the other from its superior laryngeal branch, passing then toward the carotid artery and taking its course down the neck by the side of the sympathetic as far as the thorax. In the chest, it joins with sympathetic filaments to pass with them to the heart, by little branches between the origin of the aorta and the pulmonary artery. This nerve can be completely isolated in the neck from the sympathetic and the trunk of the pneumogastric. If it be divided in this situation, after the irritation produced by the operation has subsided, very distinct and important modifications in the circulation may be produced by its galvanization.

In the first place, it was noted in all the experiments, that galvanization of the peripheral extremities produced no change, either in the number of the pulsations of the heart or in the pressure of blood in the vascular system; which points to the fact that its action is not direct, but reflex, and that it is due to an impression conveyed to the nerve-centres.

If the central ends of the nerves be galvanized, the pressure in the arteries diminishes little by little, until it may be reduced to one-half or two-thirds of the pressure before the irritation was applied. This low pressure continues so long as the interrupted current is applied; but, when the galvanization is arrested, it gradually returns to the normal standard. These phenomena are observed in all the large arterial trunks. The length of time required to produce the greatest diminution in the pressure is somewhat variable, but the experimenters have never seen it reach its minimum before fifteen pulsations of the heart.

"The diminution in the pressure is attended with a reduction of the pulse in the instances in which the depressor-nerve only has been divided. The irritated nerve is isolated in a manner so complete that we cannot fear the passage of the exciting current in the trunk of the pneumogastric. The changes in the number of pulsations persist even when the pneumogastric has been excited by the side where the irritation has been applied, from the point where the superior laryngeal is given off to the point where the pneumogastric enters the thoracic cavity.

"From the foregoing it is evident that the changes taking place in the number of pulsations are due to excitation of the depressor-nerve. If we study attentively the progress of the cardiac pulsations during the excitation, we observe always that the most considerable reduction takes place at the beginning of the experiment; that is to say, at the moment when the blood-pressure descends from its normal standard to the lowest point. When the pressure is completely depressed, the pulse is accelerated again and even reaches almost completely the numbers presented before the oscillations. When the irritation ceases, after a shorter or longer period, the heart generally beats more rapidly than before the irritation, and this during all the time that is occupied in the return of the pressure to the normal standard. This observation in itself refutes the idea that the diminution in the pressure may depend upon the diminished number of pulsations. If the reduction in the rate of the pulse produced a diminished pressure, it should be increased when the pulsations of the heart become accelerated.

"The manner in which the pulse is reduced leads to the supposition that it is due to a reflex action of the pneumogastric.

"It was easy to verify this last opinion, and we have been able to confirm it by first cutting the pneumogastrics on both sides, and afterward irritating the central end of the depressor-nerve. In this case, the pressure fell to 0·62, 0·55, etc., while the number of pulsations remained the same, or at least oscillated very slightly above and below the number observed before the irritation."

The above extract from the observations of Cyon shows two important points:

First, galvanic stimulation of the central extremities of the divided depressor-nerves reduces the number of pulsations of the heart by a reflex action; the impression being conveyed to the nerve-centres by the depressor-nerves, and the force operating directly upon the heart being transmitted through efferent filaments in the trunk of the pneumogastric.

Second, the reduction in the pressure of blood in the larger arteries is independent of the efferent filaments of the pneumogastric and bears no relation to the reduction in the number of cardiac pulsations.

It now remains to explain, if possible, the mechanism of the reduction in the arterial pressure. This question is treated by Cyon by the method of exclusion. The diminution in the pressure followed galvanization of the central extremities of the depressor-nerves, even when the heart was removed from its influence by section of both pneumogastrics in the neck, and when all the voluntary movements and the movements of respiration were abolished by poisoning with woorara. In the latter case, the circulation was kept up by artificial respiration. Without following out the various observations which go to show that the influence of the depressor-nerve upon the arterial pressure is independent of the force or frequency of the heart's action and is due to some cause which operates upon the vessels themselves, we shall simply give the results of the experiments upon the splanchnic nerves. If the abdomen be opened, and one or more of these nerves be divided, the arterial pressure is immediately diminished. After this, if the peripheral extremities of the divided nerves be galvanized, the pressure rapidly returns to the normal standard. These experiments "demonstrate that the splanchnic nerves constitute the most important vaso-motor nerves in the entire organism." This point being settled, the depressor-nerves were galvanized after section of the splanchnic nerves, in some cases exaggerating the general arterial pressure by compressing the aorta, and in others, leaving the aorta free. "The irritation of the depressor-nerve after section of the splanchnic nerve produced still a diminution in the blood-pressure, but the absolute value of this diminution is much less than it was during the irritation of the depressor-nerve before the section of the splanchnic." These experiments show pretty conclusively that the diminished pressure in the arterial system following stimulation of the central ends of the depressor-nerves after division is due to a reflex action on the blood-vessels of the abdominal organs, taking place through the splanchnic nerves. We are sufficiently familiar with reflex paralyzing action upon the blood-vessels through the sympathetic system; and, when we call to mind the immense extent of the abdominal vascular system, we can readily understand how, if the resistance to the flow of blood be diminished by paralysis of the muscular coats of the small arteries, the pressure in the larger arteries would be reduced.

Mechanism of the Influence of the Pneumogastrics upon the Action of the Heart.—It is useless to speculate upon the exact mechanism of the action of the pneumogastrics upon the heart. Although various explanations have been presented of the effects following division of the nerves in the neck, and of the opposite phenomena which attend the galvanization of their peripheral ends, they are all more or less unsatisfactory. All that can be said, in the present state of our knowledge, is, that the pneumogastrics, by virtue of the communicating branches from the spinal accessories, have a direct inhibitory influence upon the heart. When they are divided and the heart is removed from their influence, the pulsations become more rapid. When the peripheral ends of the divided nerves are galvanized, the heart beats more slowly, or its action may be arrested by a current of sufficient power. This action may also be reflex, due to an impression conveyed to the centres by the depressor-nerves.

Properties and Functions of the Pulmonary Branches, and Influence of the Pneumogastrics upon Respiration.—The trachea, bronchi, and the pulmonary structure are supplied with motor and sensory filaments by branches of the pneumogastrics. The recurrent laryngeals supply the upper, and the pulmonary branches, the lower part of the trachea, the lungs themselves being supplied by the pulmonary branches alone. The sensibility of the mucous membrane of the trachea and bronchi is due to the pneumogastrics, for these parts are insensible to irritation when the nerves have been divided in the neck. Longet has shown that, while an animal coughed and showed signs of pain when the mucous membrane of the respiratory passages was irritated, after division of the pneumogastrics there was no evidence of sensibility, even when the tracheal mucous membrane was treated with strong acid, or even cauterized. He also saw the muscular fibres of the small bronchial tubes contract when a galvanic stimulus was applied to the branches of the pneumogastrics.

The main interest, in this connection, is attached to the pulmonary branches and their relations to the respiratory acts. These are undoubtedly connected with important reflex phenomena, acting as centripetal nerves; and their direct action in respiration is probably much less important. They are exposed and operated upon in living animals with so much difficulty, that we know little of the direct effects of their irritation and must judge of their general properties chiefly by experiments showing their action upon respiration. We shall have to study, in connection with the functions of these nerves, the effects of their division, upon the lungs and the respiratory acts, and the phenomena, referable to the respiratory organs, which follow their galvanization. We shall also consider certain theoretical views with regard to their action in the automatic processes of respiration, and with the sense of want of air (*besoin de respirer*), which gives rise to the reflex respiratory acts.

Effects of Division of the Pneumogastrics upon Respiration.—Section of both pneumogastrics in the neck, in mammals and birds, is usually followed by death, in from two to five days. In young animals, death may occur almost instantly, from paralysis of the respiratory movements of the glottis, a fact which we have already noted in connection with the recurrent laryngeal nerves.

Very little of importance, with regard to the functions of the pneumogastrics in connection with respiration, has been ascertained by the numerous experiments on record of section of one or both of these nerves in the cervical region. It has been found by all experimenters, that animals survived and presented no very distinct abnormal phenomena after section of one nerve. Longet states that animals operated upon in this way present hoarseness of the voice and a slight increase in the number of respiratory acts. Some observers have found the corresponding lung partly emphysematous and partly engorged with blood, and others have not noted any change in the pulmonary structure.

When both nerves are divided in full-grown dogs, an experiment which we have often repeated, the effect upon the respiratory movements is very marked. For a few seconds, the number of respiratory acts may be increased; but, as soon as the animal becomes tranquil, the number is very much diminished, and the movements change their character. The inspiratory acts become unusually profound and are attended with excessive dilatation of the thorax. The animal is generally quiet and indisposed to move. We have seen, under these conditions, the number of respirations fall from sixteen or eighteen to four per minute.

In most animals that die from section of both pneumogastrics, the lungs are found engorged with blood, and, as it were, carnified, so that they sink in water. This curious fact, although its physiological significance is not apparent, has been the subject of much speculation and experimental research. Bernard found that the pulmonary lesion did not exist in birds, although section of both nerves was fatal. It had previously been ascertained that, in some animals, death takes place with no alteration of the lungs. When the entrance of the secretions into the air-passages was prevented by the introduction of a canula into the trachea, the carnification of the lungs was nevertheless observed. Without detailing all of the experiments upon which the explanation offered by Bernard is based, it is sufficient to state that he observed a traumatic emphysema as a consequence of the excessively labored and profound inspirations. Indeed, this can be actually seen when the pleura is exposed in living animals. As a result of this distention of the air-cells, the pulmonary capillaries are ruptured in different parts, the blood becomes coagulated, and the lungs are finally carnified. This cannot occur in birds, because the lungs are fixed, and their relations are such that they are not exposed to excessive distention in inspiration.

There is no satisfactory explanation of the remarkable changes in the respiratory movements that follow section of the pneumogastrics.

In this connection we may note a curious fact, observed by Prof. Dalton and others, that the pneumogastrics sometimes reunite after division. In January, 1874, we divided both pneumogastrics in a medium-sized dog. The pulse was immediately increased from one hundred and twenty to two hundred and forty in the minute, and the number of respirations fell from twenty-four to four or six. In ten days, the pulse and respirations had become normal. The dog was then killed by section of the medulla oblongata, and the reunion of the divided ends of the nerves was found to be nearly complete.

Sense of Want of Air.—The pneumogastrics may regulate the respiratory acts, but they are not the medium through which the sense of want of air (*besoin de respirer*), which gives rise to the reflex movements of respiration, is conveyed to the nerve-centres. If it be true, as it undoubtedly is, that section of both pneumogastrics in the neck modifies the number and the character of the respirations, and that, after division of the nerves, galvanization of their central ends arrests respiration, it is more than probable that this function is normally influenced through these nerves, by impressions conveyed to the centres; but precisely what this influence is or what is the mechanism of its action, we do not know.

The positive statement that the sense of want of air is not conveyed to the nerve-centres through the pneumogastrics is based, to a great extent, upon our own experiments, which have been fully detailed under the head of respiration; and we shall here give simply their results and the conclusions to which they lead.

The acts of respiration are involuntary, although they may be modified, within certain limits, through the will; and they are reflex, due to an impression conveyed to the respiratory nervous centre, the medulla oblongata, which gives rise to the stimulus that excites the action of the inspiratory muscles. It has been conclusively shown by experiments that, if artificial respiration be efficiently carried on in a living animal, so as to supply air fully to the system, the sense of want of air is not appreciated, and the animal makes no effort to breathe; but, if respiration be imperfectly performed, the animal almost immediately feels the want of air, and, in our experiments, the exposed respiratory muscles were thrown into violent but ineffectual contraction.

The principal points with reference to the location of the sense of want of air and its transmission to the nerve-centres, developed by our own experiments, are the following:

A dog was etherized, the chest was opened, exposing the heart and lungs, and artificial respiration was carried on by means of a bellows secured in the trachea. So long as the supply of air was sufficient, the animal made no effort to breathe, even when allowed to come from under the influence of the anæsthetic.

An artery was then exposed and the color of the blood noted. When the artificial respiration was arrested, the animal made efforts to breathe as soon as the blood became dark in the arterial system. We concluded from this, that the impression conveyed to the respiratory nervous centre, giving rise to the movements of respiration, was due to the action of non-oxygenated blood.

To ascertain whether the impression were made upon the nerves distributed to the lungs or upon other nerves, a large vessel was divided and the system was drained of blood, the lungs being continually supplied with fresh air. In this case, respiratory efforts of the most violent character were invariably noted following the hæmorrhage. This portion of the experiment demonstrated that the sense of want of air was not dependent upon the accumulation of carbonic acid in the lungs, but was due to a deficient supply of the oxygen-carrying fluid to the general system. It farther demonstrated that the impression in the general system was not due to the presence of carbonic acid, but to the absence of oxygen; for no blood containing carbonic acid circulated in the system.

These phenomena were observed without any modification, after division of both pneumogastric nerves in the neck, and they seem to prove conclusively that the sense of want of air is not transmitted to the respiratory nervous centre through the medium of these nerves.[1]

Effects of Galvanization of the Pneumogastrics upon Respiration.—The phenomena which follow galvanization of the pneumogastrics, although they are curious and interesting, do not throw much light upon the relations of these nerves to respiration. We have already mentioned the arrest of the respiratory movements by galvanization of the superior laryngeal branches and of the central ends of the pneumogastrics after their division in the neck. The main point of interest in this connection is the fact that the effects observed are entirely reflex, galvanization of the peripheral ends of the divided nerves having no direct action on the movements of the thorax.

In view of the very indefinite physiological applications of the experiments made by galvanizing the nerves, we shall not give in detail the numerous observations upon this subject, but shall simply state the results, as given in a recent and very elaborate work upon respiration, by M. Bert:

"1. Respiration may be arrested by excitation of the pneumogastrics (Traube), of the larynx (Cl. Bernard), of the nostrils (M. Schiff), of most of the sensory nerves (M. Schiff, an assertion that I have not been able to verify).

"2. This arrest may take place either in inspiration or in expiration, through any one of these nerves, without attributing it to the action of derived currents.

"3. A feeble excitation accelerates the respiration; a more powerful excitation retards it; a very powerful excitation arrests it. These words 'feeble' and 'powerful' having, it is understood, only a relative sense for any one animal and under certain conditions: what is feeble for one would be powerful for another, etc.

"I believe, in opposition to the opinion of Rosenthal, that section of the pneumogastrics does not increase the difficulty of arresting respiration; at least, death by excitation occurs much more easily in this case.

"4. When the respiratory movements are completely arrested, it is always the same for the general movements of the animal, which remains motionless.

"5. Respiration returns even during excitation, and when this is arrested, it almost always becomes accelerated.

"6. Arrest in expiration is more easily obtained than arrest in inspiration; there are animals, indeed, in which it is impossible to effect the latter.

"7. If an excitation be employed sufficiently powerful to arrest respiration in inspiration, all respiratory movements may be made to cease at the very moment when the excitation is applied (inspiration, half-inspiration, expiration), either by operating upon the pneumogastric, or operating upon the laryngeal. . . .

"Any feeble excitation of centripetal nerves increases the number of the respiratory movements; any powerful excitation diminishes them. A powerful excitation of the pneumogastrics, of the superior laryngeal, of the nasal branch of the infra-orbital, may arrest them completely; if the excitation be sufficiently energetic, the arrest takes place at the very moment it is applied. Finally, sudden death of the animal may follow a too powerful impression, thus transmitted to the respiratory centre: all this being true for certain mammalia, birds, and reptiles."

[1] For a full account of these experiments, with their bearing upon certain respiratory phenomena before birth, the reader is referred to the original article, entitled *Experimental Researches on Points connected with the Action of the Heart and with Respiration*, published in the *American Journal of the Medical Sciences*, Philadelphia, October, 1861. Since this publication, the experiments have been frequently repeated in public demonstrations, and the conclusions verified.

The above formulated statements express the experimental facts at present known with regard to the influence of the pneumogastrics upon respiration. The pulmonary branches themselves are so deeply situated that they have not as yet been made the subject of direct experiment, with any positive and satisfactory results.

Properties and Functions of the Œsophageal Nerves.—The muscular walls and the mucous membrane of the œsophagus are supplied entirely by branches from the pneumogastrics. The upper portion is supplied by filaments from the inferior laryngeal branches, the middle portion, by filaments from the posterior pulmonary branches, and the inferior portion receives the œsophageal branches. These branches are both sensory and motor; but probably the motor filaments largely predominate, for the mucous membrane, although it is sensible to the extremes of heat and cold, the feeling of distention, and a burning sensation upon the application of strong irritants, is by no means acutely sensitive.

That the movements of the œsophagus are animated by branches from the pneumogastrics, has been clearly shown by experiments. In the first place, except in animals in which the anatomical distribution of the nerves is different from the arrangement in the human subject, the entire œsophagus is paralyzed by dividing the nerves in the neck. When the pneumogastrics are divided in the cervical region, in dogs, if the animals attempt to swallow a considerable quantity of food, the upper part of the œsophagus is found enormously distended. Bernard noted in a dog in which a gastric fistula had been established, that articles of food given to the animal did not pass into the stomach, although he made great efforts to swallow. An instant after the attempt, the matters were regurgitated, mixed with mucus, but of course did not come from the stomach.

Direct experiments upon the roots of the pneumogastrics have shown that these nerves influence the movements of the œsophagus, and that the motor filaments involved do not come from the spinal accessory; but it is not known from what nerves these motor filaments are derived.

Properties and Functions of the Abdominal Branches.—In view of the very extensive distribution of the terminal branches of the pneumogastrics to the abdominal organs, it is evident that the functions of these nerves must be very important, particularly since it has been shown that the right nerve is distributed to the whole of the small intestine. We shall consider the functions of these branches in their relations to the liver, the stomach, and the intestines. We have no positive information with regard to their action upon the spleen, kidneys, and suprarenal capsules.

Influence of the Pneumogastrics upon the Liver.—There is very little known with regard to the influence of the pneumogastrics upon the secretion of bile; and the most important experiments upon the innervation of the liver relate to its glycogenic function. We shall have little to say upon this subject, however, in addition to what we have already stated in treating of the liver as a sugar-producing organ. The view which we have advanced with regard to the glycogenic function is that the liver is constantly producing sugar during life, which is completely washed out by the blood in its passage through this organ, the liver itself containing little or no sugar, under normal conditions. With this view, we are to look for sugar in the blood in certain situations, and not in the liver itself; although, after death, a change of the glycogenic matter in the liver into sugar takes place with great rapidity, and sugar may then be found in its substance. Normally, sugar disappears in the lungs and is not found in the blood of the arterial system. The presence of sugar in the urine is abnormal. If both pneumogastrics be divided in the neck, and the animal be killed at a period varying from a few hours to one or two days after, the liver contains no sugar, under the conditions in which it is generally found, viz., a certain time after death. From experiments of this kind, Bernard concludes that the glycogenic function is suspended when the nerves are divided. The experiments, however, made by irritating the pneumogastrics, were more satisfactory, as in these he looked for sugar in the blood and in the urine and did not confine his examinations to the substance of the liver.

After division of the pneumogastrics in the neck, if the peripheral ends be galvanized, there is no effect upon the liver; but, if galvanization be applied to the central ends, the glycogenic function becomes exaggerated, and sugar makes its appearance in the blood and in the urine. Bernard has made a number of experiments illustrating this point, upon dogs and rabbits. The galvanic current employed was generally feeble, and it was continued for from five to ten minutes, two or three times in an hour. In some instances the irritation was kept up for thirty minutes. From these experiments, it is assumed that the physiological production of sugar by the liver is reflex and is due to an impression conveyed to the nerve-centres through the pneumogastrics. A very interesting and adroit experiment by the same observer shows that section of the pneumogastrics between the lungs and the liver does not affect the production of sugar. This delicate operation is performed by making a valvular opening in the chest, preventing the ingress of air by suddenly forcing the finger into the wound, and then introducing a long, delicate hook with a cutting edge, and dividing the nerves, which may be reached by the finger in small dogs, and feel like tense cords by the side of the œsophagus. We have already noted that the inhalation of irritating vapors and of anæsthetics produces a hypersecretion of sugar by the liver.

The remarkable effects of irritating the floor of the fourth ventricle, by which we can produce temporary diabetes, have been considered fully in connection with the glycogenic function of the liver. This effect is not due to a direct transmission of the irritation to the liver through the pneumogastrics, for the phenomena of hypersecretion are observed in animals upon which this operation has been performed after section of both pneumogastrics in the neck. It is probable, indeed, that the impression is conveyed to the liver through the sympathetic system, for it has been shown that animals do not become diabetic after irritation of the floor of the fourth ventricle, when the branches of the sympathetic going to the solar plexus have been divided. The operation, however, of dividing the sympathetic nerves in this situation is so serious, that it may interfere with the experiment in some other way than by the direct influence of the nerves upon the liver.

Influence of the Pneumogastrics upon the Stomach and Intestines.—The number of observations that have been made upon the influence of the pneumogastric nerves on digestion in the stomach is immense, and many of the earlier experiments were quite contradictory. We do not propose, however, to treat of this subject from a purely historical point of view, for the reason that, before 1842 and 1843, when gastric fistulæ were first established in living animals, little was known of the normal movements of the stomach and of the mechanism of the secretion of the gastric juice; and, farthermore, before the observations of Bouchardat and Sandras, in 1847, the effects of section of the nerves in the neck upon the action of the œsophagus in deglutition were not understood. If we study the literature of the subject anterior to 1842, we find a great deal of confusion, due to the facts just stated. Leaving out of the question most of the earlier experiments, we shall treat of the influence of the pneumogastrics upon the stomach and intestines, under the following heads:

1. The effects of galvanization of the nerves.
2. The effects of section of the nerves upon the movements of the stomach in digestion.
3. The effects of section of the nerves upon the secretion of the gastric juice and the chemical processes of digestion.
4. The influence of the nerves upon the small intestine.

Effects of Galvanization.—As the result of recent experiments, the effects of galvanization of the pneumogastrics upon the movements of the stomach are unquestionable. Longet has shown that the stomach contracts as a consequence of irritation of the nerves, not instantly, but after the lapse of five or six seconds. He explains some of the contradictory results obtained by other observers by the fact that these contractions are very marked during stomach-digestion, while they are wanting "when the stomach is entirely empty, retracted on itself and in a measure in repose." According to the same author, irritation of the splanchnic nerves, while it produces movements of the intestines, does not affect the stomach. Judging from the tardy contraction of the stomach and the analogy between the action of the pneumogastrics upon this organ and the action of the sympathetic nerves upon the non-striated muscular tissue, Longet assumes that the motor action of the pneumogastrics is due, not to the proper filaments of these nerves, but to filaments derived from the sympathetic system. "This interpretation removes the singular physiological anomaly that an organ, the action of which is entirely removed from the control of the will, should depend upon a voluntary, or cerebro-spinal nerve." This explanation of the contradictory results of experiments and of the mechanism of the action of the pneumogastrics upon the stomach seems entirely satisfactory and may be accepted without reserve.

Effects of Section of the Pneumogastrics upon the Movements of the Stomach.—If the pneumogastrics be divided in the neck in a dog in full digestion, in which a gastric fistula has been established so that the interior of the organ can be explored, the following phenomena are observed:

In the first place, before division of the nerves, the mucous membrane of the stomach is turgid, its reaction is intensely acid, and, if the finger be introduced through the fistula, it will be firmly grasped by the contractions of the muscular walls. When the pneumogastrics are divided, under these conditions, the contractions of the muscular walls instantly cease, the mucous membrane becomes pale, the secretion of gastric juice is apparently arrested, and the sensibility of the organ is abolished. Paralysis of the stomach, etc., had been noted, long before the observations of Bernard; but his experiments upon animals with a fistulous opening into the stomach are the most striking.

Notwithstanding the apparent arrest of the movements of the stomach in digestion by section of the pneumogastrics, experiments carefully performed show that substances may be very slowly passed to the pylorus, and that the movements, although they are greatly diminished in activity, are not entirely abolished. This fact has been established beyond question by the experiments of Schiff, who attributes the movements occurring after section of the nerves to local irritation of the intramuscular terminal nervous filaments.

Effects of Section of the Pneumogastrics upon Digestion, etc.—When both nerves are divided, in an animal in full digestion, the mucous membrane becomes pale and flaccid, and the secretion of gastric juice is apparently arrested at once; but, if the animal survive the operation for a day or two, a certain quantity of juice may be secreted as the result of local stimulation, and digestion of a very small quantity of food, finely divided and introduced into the stomach by a fistulous opening, may take place. A serious difficulty in the digestion of large masses of food after division of the nerves is due to the cessation of the movements of the stomach. It is stated that digestion may be to a certain extent reëstablished, under these conditions, by galvanizing the peripheral extremities of the divided nerves.

There is very little to be said with regard to the relations of the pneumogastrics to the sensations of hunger and thirst. It would be very natural to infer, from the distribution of these nerves to the mucous membrane of the stomach, that they should be involved in these sensations; but, in treating of this subject elaborately, in connection with alimentation, we have shown that hunger and thirst really have their origin in the general system, although the sensations are referred subjectively to the stomach and fauces, and that, in all probability, the sensations persist after division of both pneumogastrics.

With regard to the influence of the pneumogastrics upon absorption from the stomach, we have also mentioned the fact that the passage of poisons from the stomach into the blood-vessels may be retarded by section of the nerves, but is not prevented.

Physiologists have given but little attention to the influence of the pneumogastrics upon the intestinal canal, for the reason that the distribution of the abdominal branches to the small intestine, notwithstanding the researches of Kollmann, in 1860, does not appear to have been generally recognized. The right, or posterior abdominal branch was formerly supposed to be lost in the semilunar ganglion and the solar plexus, after sending a few filaments to the stomach; but, since it has been shown that this nerve is supplied to the whole of the small intestine, its physiology, in connection with intestinal secretion, has assumed considerable importance.

In a series of experiments, by Prof. Horatio C. Wood, Jr., of Philadelphia, the importance of the abdominal branches of the right nerve is fully illustrated. These experiments show, in the most conclusive and satisfactory manner, that the pneumogastrics influence intestinal as well as gastric secretion. One of the most interesting and curious points in connection with their function is that, after section of the nerves in the cervical region, the most powerful cathartics, croton-oil, calomel, podophyllin, jalap, arsenic, etc., fail to produce purgation, even in doses sufficient to cause death. The articles used were either given by the mouth, just before dividing the nerves, or were injected under the skin.

Although the observations of Dr. Wood are not entirely new, they are by far the most extended and satisfactory, and were made with a knowledge of the fact of the distribution of the nerves to the small intestine. Dr. Wood quotes freely from the experiments made by Sir Benjamin Brodie and by Dr. John Reid. Brodie failed to produce purging in dogs, when both pneumogastrics had been divided in the neck, after the administration of arsenic by the mouth and after injecting it under the skin. Dr. Reid made five experiments, and, in all but one, it is stated that diarrhœa existed after division of the nerves. In twenty experiments by Dr. Wood, there was no purgation after division of the nerves, in one there was free purgation, and in one there was "some slight muco-fecal discharge." From these, Dr. Wood concludes that, while section of the cervical pneumogastrics, in the great majority of instances, arrests gastro-intestinal secretion and prevents the action of purgatives upon the intestinal canal, a few exceptional cases occur in which these effects are not observed.

The facts just mentioned are exceedingly interesting in connection with the experiments of Traube upon the action of digitalis after section of the pneumogastrics. It will be remembered that, in these experiments, digitalis failed to diminish the number of beats of the heart when the nerves had been divided in the neck, showing that the separation of the heart from its connections with the cerebro-spinal system removed the organ from the peculiar and characteristic effects of the poison.

It would be interesting to determine whether the pneumogastrics influence the intestinal secretions through their own fibres or through filaments received from the sympathetic system; but there are no experimental facts sufficiently definite to admit of a positive answer to this question. If the action take place through the sympathetic system, as in the case of the stomach, the filaments of communication join the pneumogastrics high up in the neck.

CHAPTER XX.

FUNCTIONS OF THE SPINAL CORD.

General arrangement of the cerebro-spinal axis—Membranes of the encephalon and spinal cord—Cephalo-rachidian fluid—Physiological anatomy of the spinal cord—Direction of the fibres after they have penetrated the cord by the roots of the spinal nerves—General properties of the spinal cord—Action of the spinal cord as a conductor—Transmission of motor stimulus in the cord—Decussation of the motor conductors of the cord—Transmission of sensory impressions in the cord—The white substance of the posterior columns does not conduct sensory impressions—Action of the gray matter as a conductor—Probable function of the cord in connection with muscular co-ordination—Decussation of the sensory conductors of the cord—Summary of the action of the cord as a conductor—Action of the spinal cord as a nerve-centre—Movements in decapitated animals—Definition and applications of the term "reflex"—Reflex action of the spinal cord—Question of sensation and volition in frogs after decapitation—Character of movements following irritation of the surface in decapitated animals—Dispersion of impressions in the cord—Conditions essential to the manifestation of reflex phenomena—Exaggeration of reflex excitability by decapitation, poisoning with strychnine, etc.—Reflex phenomena observed in the human subject.

UNDER the head of special senses, we shall consider, in succeeding chapters, the properties and functions of the first and second nerves, the portio mollis of the seventh, or auditory, and the gustatory nerves, comprising a part of the glosso-pharyngeal and a small filament from the facial (the chorda tympani) going to the lingual branch of the fifth. This will include a full account of the organs of smell, taste, sight, and hearing, with a description of the general sensory nerves, as far as they are concerned in the sense of touch. We shall here begin our history of the cerebro-spinal axis, which will include the physiological anatomy, properties, and functions of the encephalon and the spinal cord.

General Arrangement of the Cerebro-spinal Axis.—The nervous matter contained in the cavity of the cranium and in the spinal canal, exclusive of the roots of the cranial and spinal nerves, is known as the cerebro-spinal axis. This portion of the nervous system is composed of white and gray nervous matter. The fibres of the white matter act as conductors. The gray matter constitutes a chain of ganglia, which act as nerve-centres, receiving impressions and generating the so-called nerve-force. The gray matter of the spinal cord also serves, to a greater or less extent, as a conductor.

The cerebro-spinal axis is enveloped in membranes, which are for its protection and for the support of its nutrient vessels. It is surrounded, to a certain extent, with liquid, and it presents cavities, as the ventricles of the brain and the central canal of the chord, which contain liquid. The gray matter is distinct from the white, even to the naked eye. In the spinal cord, the white substance is external and the gray is internal. The surface of the brain presents an external layer of gray matter, the white substance being internal. In the white substance of the brain, also, we find collections of gray matter. As we should expect, from the similarity in function between the white matter and the nerves, this portion of the cebro-spinal axis is composed largely of fibres. The gray substance is composed chiefly of cells.

The encephalon is contained in the cranial cavity. In the human subject and in many of the higher animals, its surface is marked by numerous convolutions, by which the extent of its gray substance is very much increased. The cerebrum, the cerebellum, and all of the encephalic ganglia are connected with the white substance of the encephalon and with the spinal cord. With the encephalon and the cord, all of the cerebro-spinal nerves are connected. The cerebro-spinal axis acts as a conductor, and its different collections of gray matter, or ganglia, receive impressions conveyed by the sensory conducting fibres, and generate nerve-force, which is transmitted to the proper organs by the motor fibres.

Membranes of the Encephalon and Spinal Cord.—The membranes of the brain and spinal cord are, the dura mater, the arachnoid, and the pia mater.

The dura mater of the encephalon is a dense, fibrous membrane, in two layers, composed chiefly of inelastic tissue, which lines the cranial cavity and is adherent to the bones. In certain situations, its two layers become separated and form what are known as the venous sinuses. The dura mater also sends off folds or processes of its internal layer. One of these passes into the longitudinal fissure and is called the falx cerebri; another lies between the cerebrum and the cerebellum and is called the tentorium; another is situated between the lateral halves of the cerebellum and is called the falx cerebelli. The dura mater is closely attached to the bone at the border of the foramen magnum. From this point it passes into the spinal canal and forms a loose covering for the cord. In the spinal canal, this membrane is not adherent to the bones, which have, like most other bones in the body, a special periosteum. At the foramina of exit of the cranial and the spinal nerves, the dura mater sends out processes which envelop the nerves, with the fibrous sheaths of which they soon become continuous.

The arachnoid is an excessively delicate serous membrane, in two layers, the surfaces of which are nearly in contact. The external layer lines the internal surface of the dura mater. Like the other serous membranes, the arachnoid is covered with a layer of tesselated epithelium. There is a small amount of liquid between the two layers of the arachnoid; but by far the greatest quantity of liquid surrounding the cerebro-spinal axis lies beneath both layers, in what is called the subarachnoid space. This is called the cerebro-spinal, or cephalo-rachidian fluid. The arachnoid does not follow the convolutions and fissures of the encephalon or the sulci of the cord, but it simply covers their surfaces. Magendie pointed out a longitudinal, incomplete, cribriform, fibrous septum in the cord, passing from the inner layer of the arachnoid to the pia mater. A similar arrangement is found in certain situations at the base of the skull.

The pia mater of the encephalon is a delicate, fibrous structure, exceedingly vascular, seeming to present, indeed, only a skeleton net-work of fibres for the support of the vessels going to the nervous substance. This membrane covers the surface of the encephalon immediately, follows the sulci and fissures, and is prolonged into the ventricles, where it forms the choroid plexus and the velum interpositum. From its internal surface, small vessels are given off which pass into the nervous substance.

The pia mater of the encephalon is continuous with the corresponding membrane of the cord; but, in the spinal canal, it is thicker, stronger, more closely adherent to the subjacent parts, and its blood-vessels are by no means so numerous. In this situation, many of the fibres are arranged in longitudinal bands. This membrane lines the anterior sulcus and a portion of the posterior sulcus of the cord. It is sometimes spoken of as the neurilemma of the cord. At the foramina of exit of the cranial and the spinal nerves, the fibrous structure of the pia mater becomes continuous with the nerve-sheaths.

Between the anterior and posterior roots of the spinal nerves, on either side of the cord, is a narrow, ligamentous band, the ligamentum denticulatum, which assists in holding the cord in place. This extends from the foramen magnum to the terminal filament of the cord, and is attached, internally, to the pia mater, and externally, to the dura mater.

It is not necessary to enter into a detailed description of the arrangement of the blood-vessels, nerves, and lymphatics of the membranes of the brain and spinal cord, or of the vascular arrangement in the substance of the cerebro-spinal axis, as these points are chiefly of anatomical interest. The circulation in these parts presents certain peculiarities. In the first place, the encephalon being contained in an air-tight case of invariable capacity, it has been a question whether or not the vessels be capable of contraction and dilatation, or whether the quantity of blood in the brain be subject to modifications in health or disease. These questions may certainly be answered in the affirmative. In infancy and in the adult, when an opening has been made in the skull, the volume of the encephalon is evidently increased during expiration and is diminished in inspiration. Under normal conditions, in the adult, it is probable that the amount of blood is increased

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in expiration and diminished in inspiration; but it is not probable that the cerebro-spinal axis undergoes any considerable movements. The important peculiarities in the cerebral circulation have already been fully considered in connection with the circulation. It has been shown that the encephalic capillaries are surrounded or nearly surrounded by canals (perivascular canal-system), which exceed the blood-vessels in diameter by from $\frac{1}{1200}$ to $\frac{1}{400}$ of an inch, and are connected with lymphatic trunks or reservoirs situated under the pia mater. The system of canals may, by variations in its contents, serve to equalize the amount of liquid in the brain as the blood-vessels are distended or contracted.

Cephalo-rachidian Fluid.—The greatest part of the fluid in the cranium and in the spinal canal is contained in what is known as the subarachnoid space; that is, between the inner layer of the arachnoid and the pia mater, and not between the two layers of the arachnoid. The ventricles of the encephalon are in communication with the central canal of the cord, and are also connected with the general subarachnoid space, by a narrow, triangular orifice, situated at the inferior angle of the fourth ventricle. By this arrangement, the liquid in the ventricles of the encephalon and in the central canal of the cord communicates with the liquid surrounding the cerebro-spinal axis, and the pressure upon these delicate parts is equalized.

As far as we know, the function of the cephalo-rachidian fluid is simply mechanical, and its properties and composition have no very definite physiological significance. Its quantity was estimated by Magendie, in the human subject, at about two fluidounces; but this was the smallest amount obtained by placing the subject upright, making an opening in the lumbar region and a counter-opening in the head to admit the pressure of the atmosphere. The exact quantity in the living subject could hardly be estimated in this way; and it is difficult, indeed, to see how any thing more than a roughly approximative idea could be obtained. The quantity obtained by Magendie probably does not represent the entire amount of liquid contained in the ventricles and in the subarachnoid space, but it is the most definite estimate that has been given.

The discharge of a certain quantity of the cephalo-rachidian fluid does not produce any marked derangement in the action of the nervous system. When the liquid is allowed to flow spontaneously through a small trocar introduced without division of the muscles of the neck, there follows no serious nervous disturbance; but, when the liquid is drawn out forcibly with a syringe, the animal first becomes enfeebled and afterward seems affected with general paralysis. These phenomena are probably due, not so much to removal of the fluid, as to congestion of blood-vessels and even effusion of blood, which follow sudden diminution in the pressure. Sudden increase in the quantity of liquid surrounding the cerebro-spinal axis produces coma, probably from compression of the centres. This fact was demonstrated by Magendie, by injecting water in animals, and also by compressing the tumor, in cases of spina bifida in the human subject, by which the fluid was pressed back into the spinal canal. In the cases of spina bifida, the subject, during the compression, fell into coma, which was instantly relieved by removing the pressure. The cephalo-rachidian fluid is speedily reproduced after its evacuation. In all probability it is secreted by the pia mater.

The general properties and composition of the fluid under consideration are, in brief, the following: It is perfectly transparent and colorless, free from viscidity, of a distinctly saline taste, alkaline reaction, and it resists putrefaction for a long time. It is not affected by heat or acids. As we should expect from its low specific gravity and purely mechanical function, it contains a large proportion of water (981 to 985 parts per thousand). It contains a considerable quantity of chloride of sodium, a trace of chloride of potassium, sulphates, carbonates, and alkaline and earthy phosphates. In addition, it contains traces of urea, glucose, lactate of soda, fatty matter, cholesterine, and albumen.

As a summary of the function of the cephalo-rachidian fluid, it may be stated, in general terms, that it serves to protect the cerebro-spinal axis, chiefly by equalization of the pressure in the varying condition of the blood-vessels, accurately filling the space between the centres and the bony cavities in which they are contained. That the blood-vessels of the cerebro-spinal axis are subject to variations in tension, is readily shown by introducing a canula into the subarachnoid space, when the jet of fluid discharged will be increased with every violent muscular effort. The pressure of the fluid, in this instance, could only be affected through the blood-vessels.

Physiological Anatomy of the Spinal Cord.

The spinal cord, with its membranes, the roots of the spinal nerves, and the surrounding liquid, occupies the spinal canal and is continuous with the encephalon. Its length is from fifteen to eighteen inches, and its weight is about an ounce and a half. Its form is cylindrical, being slightly flattened in certain portions. It extends from the foramen magnum to the first lumbar vertebra. It presents, at the origin of the brachial nerves, an elongated enlargement, and a corresponding enlargement at the origin of the nerves which supply the lower extremities. It terminates below in a slender, gray filament, called the filum terminale. The sacral and coccygeal nerves, after their origin from the lower portion of the cord, pass downward to emerge by the sacral foramina, and they form what is known as the cauda equina.

The substance of the cord is formed of white and gray matter, the white matter being external. The proportion of white matter to the gray is greatest in the cervical region. This fact is important in studying the course of the fibres and in view of the functions of the cord as a conductor. The inferior, pointed termination of the cord consists entirely of gray matter.

The cord is marked by an anterior and a posterior medium fissure, and by imperfect and somewhat indistinct anterior and posterior lateral grooves, from which latter arise the anterior and the posterior roots of the spinal nerves. The posterior lateral groove is tolerably well marked, but there is no distinct line at the origin of the anterior roots. The anterior median fissure, or sulcus, is perfectly distinct. It penetrates the anterior portion of the cord in the median line for about one-third of its thickness and receives a highly vascular fold of the pia mater. It extends to the anterior white commissure. The posterior fissure is not so distinct as the anterior, and it is not lined throughout by a fold of the pia mater, but is filled with connective tissue and blood-vessels, which form a septum posteriorly, between the lateral halves of the cord. The posterior median fissure, so called, extends nearly to the centre of the cord, as far as the posterior gray commissure.

Physiologically and anatomically, the cord is divided into two lateral halves; but the division of each half into columns is not so distinct. Anatomists generally regard a half of the cord as consisting of three columns: The anterior column is bounded by the anterior fissure and the origin of the anterior roots of the spinal nerves; the lateral column is included between the anterior and the posterior roots of the nerves; the posterior column is bounded by the line of origin of the posterior roots and by the posterior fissure. Some anatomists include the lateral with the anterior column, under the name of the antero-lateral column, taking in about two-thirds of the cord. Next the posterior median fissure, is a narrow band, marked by a faint line, which is sometimes called the posterior median column.

The arrangement of the white and the gray matter in the cord is seen in a transverse section. The gray substance is in the form of a letter H, presenting two anterior and two posterior cornua connected by what is called the gray commissure. The anterior cornua are the shorter and broader, and they do not reach to the surface of the cord. The posterior cornua are larger and narrow, and they extend nearly to the surface, at the point of origin of the posterior roots of the spinal nerves. In the centre of the gray commissure, is a very narrow canal, lined by cells of ciliated epithelium, called the central canal. This is in communication above with the fourth ventricle, and it extends below to the filum terminale. That portion of the gray commissure situated in front of this canal is sometimes called the anterior gray commissure, the posterior portion being known as the posterior gray commissure. The central canal is immediately surrounded by connective tissue. In front of the gray commissure, is a mass of white substance known as the anterior white commissure.

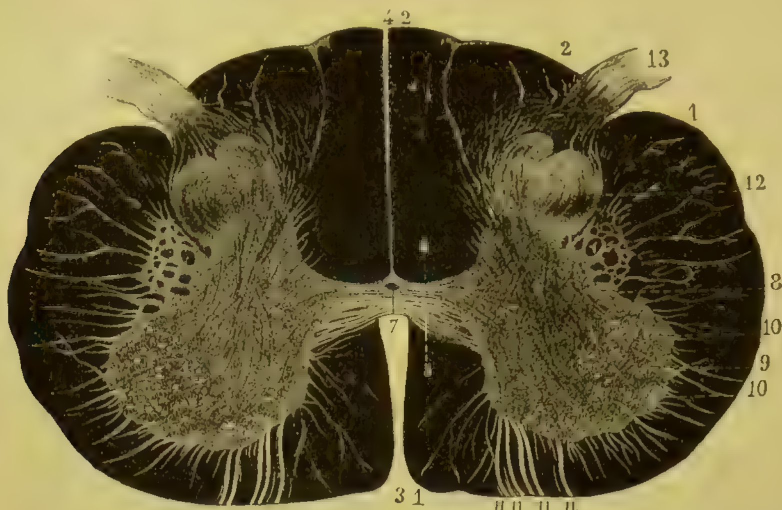


FIG. 222.—*Transverse section of the spinal cord at the origin of the fifth pair of cervical nerves.* (Stilling.) In this figure, the white substance of the cord is represented in black, to show more clearly the limits of the gray matter: 1, 1, antero-lateral columns; 2, 2, posterior white columns; 3, anterior median fissure; 4, posterior median fissure; 5, white commissure; 6, gray commissure; 7, central canal; 8, 9, anterior cornua of gray matter; 10, 10, group of large multipolar cells; 11, 11, 11, anterior roots of the spinal nerves; 12, posterior cornua of gray matter; 13, posterior roots of the spinal nerves.

The proportion of the white to the gray substance is variable in different portions of the cord. In the cervical region, the white substance is most abundant, and, in fact, it progressively increases in quantity from below upward throughout the whole extent of the cord. In the dorsal region, the gray matter is least abundant, and it exists in greatest quantity in the lumbar enlargement.

The white substance of the cord is composed of nerve-fibres, connective-tissue elements, and blood-vessels, the latter arranged in a very wide and delicate plexus. The nerve-fibres are variable in their size and are composed of the axis-cylinder surrounded by the medullary substance, without, however, the investing membrane. We shall speak farther on of the direction of the fibres in the cord.

The anterior cornua of gray matter contain blood-vessels, connective-tissue elements, very fine nerve-fibres, and large multipolar nerve-cells, which are sometimes called motor cells. The posterior cornua are composed of the same elements, the cells being much smaller, and the fibres exceedingly small, presenting very fine plexuses. The cells in this situation are sometimes called sensory cells. Near the posterior portion of each posterior cornu, is an enlargement, of a gelatiniform appearance, containing numerous small cells and fibres, called the substantia gelatinosa.

The foregoing description of the different structures and parts of the cord is necessary to a comprehension of the direction of the fibres in the spinal axis and their connections with the nerve-cells, which is the anatomical basis of our knowledge of its physiology. The connections between the cells and the fibres have already been described in the chapter upon the general structure of the nervous system. The multipolar nerve-cells are supposed to present certain prolongations which do not branch and are directly connected with the medullated nerve-fibres. These are called nerve-prolongations. In addition, fine, branching poles are described under the name of protoplasmic prolongations.

The direction of the fibres in the cord is one of the most difficult and complicated problems in physiological anatomy; and, especially as regards the posterior roots of the nerves, it is one which cannot as yet be elucidated by purely anatomical investigations, but requires the aid of experimental and pathological observations. In order to understand fully the importance of this question, it is necessary to bear in mind the following physiological facts, which it is desirable, if possible, to explain by the anatomical relations and connections of the fibres and cells:

1. The cord serves as a conductor of impressions to the brain, conveyed to it through the posterior roots, and of stimulus generated by the brain and passing from the cord by the anterior roots of the spinal nerves. This action is crossed, the decussation taking place mainly at the medulla oblongata, for the anterior portions, and throughout the whole extent of the cord, for the posterior portions.

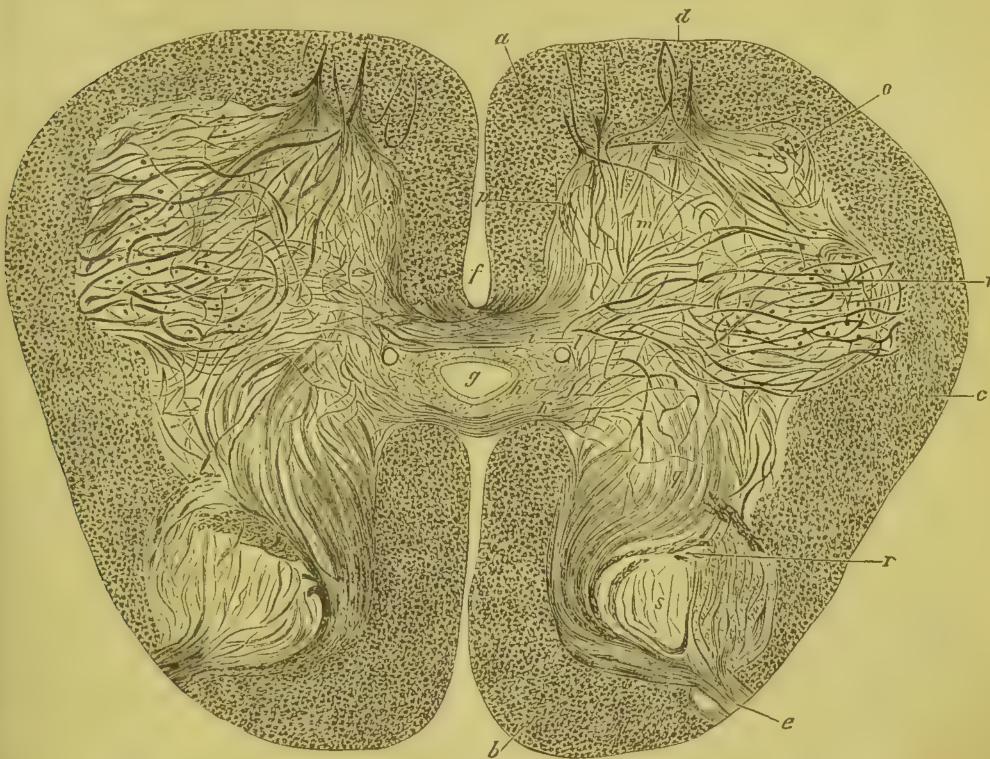


FIG. 223.—*Transverse section of the spinal cord of a child six months old, at the middle of the lumbar enlargement, treated with potassio-chloride of gold and nitrate of uranium; magnified 20 diameters. By means of these reagents, the direction of the fibres in the gray substance is rendered unusually distinct.* (Gerlach.)

a, anterior columns; *b*, posterior columns; *c*, lateral columns; *d*, anterior roots; *e*, posterior roots; *f*, anterior white commissure, in communication with the fasciculi of the anterior cornua and the anterior columns; *g*, central canal with its epithelium; *h*, surrounding connective substance of the central canal; *i*, transverse fasciculi of the gray commissure in front of the central canal; *k*, transverse fasciculi of the gray commissure behind the central canal; *l*, transverse section of the two central veins; *m*, anterior cornua; *n*, great, lateral cellular layer of the anterior cornua; *o*, lesser, anterior cellular layer; *p*, smallest, median cellular layer; *q*, posterior cornua; *r*, ascending fasciculi in the posterior cornua; *s*, substantia gelatinosa.

2. Independently of its action as a conductor, the cord, disconnected from the rest of the cerebro-spinal axis, acts as a nerve-centre, by virtue of its gray matter and the fibres connected with the cellular elements of this substance.

Bearing in mind these points, which are matters of positive demonstration, we are prepared to study the anatomical relations of the fibres and cells. In this, we shall content ourselves with the following very recent description, quoted in full from Gerlach, which embodies about all of our positive knowledge upon the subject, presented in the clearest manner possible. This extract, the translation of which is almost literal, should be carefully studied by those who desire to learn what is known at the present day with regard to the physiological anatomy of the cord. As a preparation for this study, it would be well to closely examine Fig. 223, which gives a general view of the different parts of the cord, shown in a transverse section:

"With the present methods and means of investigation at our command, we can scarcely give an exact, detailed description of the course of the fibres in the spinal cord, the groundwork of the physiology of this organ. Investigations up to this time afford at least the outlines of a sketch which, as regards the course of the fasciculi of the anterior roots, has a tolerably definite basis; and, on the other hand, with regard to the fasciculi going to the spinal cord through the posterior roots, is quite incomplete and uncertain.

"The fasciculi of the anterior roots, after their entrance into the cord, pass diagonally through the white substance, and, as such, are not at all concerned in its formation. On the contrary, they pass immediately to the gray substance of the anterior cornua, and, by their prolongations, are in direct connection with the nerve-cells in this situation, which, accordingly, are to be regarded as the elements of origin of the anterior roots in the cord. The protoplasmic processes of these nerve-cells form parts of the fine plexuses of nerve-fibres in the gray substance, from which larger nerve-fibres take their origin. These, extending in two directions, leave the gray substance, to pass up in the white substance to the brain. In consequence of the entrance of additional nerve-fibres, the white substance is necessarily increased in quantity in the cord from below upward. With regard to the course of the fasciculi which pass out of the gray substance of the anterior cornua, these are to be divided into median and lateral. The median fasciculi pass immediately into the anterior white commissure, where they decussate with corresponding fasciculi from the opposite side, to pass upward again in the anterior column of the other half of the cord. The lateral fasciculi go to the lateral columns of the same side, in which they pass to the brain, having first undergone decussation in the anterior pyramids of the medulla oblongata.

"The posterior nerve-roots enter horizontally, running in the white substance of the spinal cord, in a direction from without inward toward the median line, and here divide into two portions. The lateral portion, the smaller, retains the horizontal direction and passes through the substantia gelatinosa, dividing into fine and the finest bundles, in the manner mentioned above, to take part in the formation of the vertical bundle of fibres, which lies immediately in front. Here the fibres pass onward, a portion of them ascending and a portion descending. The fibres of the lateral portion of the posterior roots do not remain very long in the vertical bundle, but curve forward in a horizontal plane, and in this way reach the portion of the posterior cornua containing a fine plexus of nerve-fibres.

"The median (larger) portion of the posterior root-fibres passes to that portion of the posterior column which bounds the substantia gelatinosa internally and posteriorly; and curving, takes here a vertical course to pass into the posterior columns, extending chiefly upward, but perhaps downward as well. The median posterior root-fibres then undergo another deflection, by which they again take a horizontal direction, and pass to the gray substance of the posterior cornua, in part through the median portion and in part by the inner border of the substantia gelatinosa. With regard to the farther course of the posterior root-fibres, it is impossible to present positive explanations, for the reason that the present methods of investigation do not afford any means of distinguishing the posterior fibres from the nerve-tubes in the vertical fasciculi of the posterior cornua, or those passing from the gray substance into the posterior columns to ascend to the brain. The numerous divisions which the posterior root-fibres penetrating the posterior cornua immediately undergo indicate, however, that a portion of them is lost directly in the fine nerve-plexus of the gray substance. But at the same time there are numerous fibres which extend forward, and others which take a more or less wavy course toward the median line. The first, perhaps, can be regarded as posterior root-fibres, which pass in a forward direction in the nervous plexus; the latter, on the other hand, belong to the commissural fibres, which cross the median line in the gray substance in front of and behind the central canal. In my opinion, the fibres which penetrate the posterior commissure are not to be regarded as belonging directly to the posterior roots, but are to be considered as fibres which pass backward to go either to the vertical fasciculi of the gray substance or to pass to the brain in the posterior columns. If this idea be correct, and it is sustained by analogous conditions in the anterior cornua, the following view may be given of the course of the fibres of the posterior roots which penetrate the gray substance: 'A portion of the posterior root-fibres, immediately after their entrance into that portion of the gray substance which contains a nerve-plexus, is lost in this plexus; another portion extends farther forward, and, in proportion as the fibres pass forward, they likewise take part, by constant divisions, in the formation of the nerve-plexus. This plexus, in which larger and smaller nerve-cells are interspersed as it were as knotted points (*Knotenpunkte*), is in direct connection with the plexus of the anterior cornua. From these cells nerve-fibres arise, which cross the median line in the gray commissure in front of and behind the central canal, then curve backward to pass up to the brain, in part in the vertical fasciculi of the posterior cornua, in part in the posterior columns, between both of which numerous connections may exist which are as yet inextricable.' This view involves a complete decussation in the spinal cord, through the fibrous elements of the posterior roots passing into this part. Whether this be in reality a complete or a partial decussation in this situation, a part of the fibres arising from the nerve-plexus passing simply backward without crossing the median line, cannot be determined by definite anatomical investigations; but pathological researches, as well as the experimental results of that most competent observer, Brown-Séquard, are decidedly in favor of a complete decussation.

"Finally, it must be admitted that two points especially are evident:

"1. In the direction of the nerve-fibres which enter through the posterior roots, the gray substance has more numerous connections than in those which pass to the spinal cord through the anterior roots.

"2. The morphological distinction determinable between the anterior and the posterior roots is, that the former take their origin directly from the nerve-cells by means of the nerve-prolongations, while, in the latter, it is only indirect through the nerve-plexus with the protoplasmic prolongations, and in this wise they are in communication with the nerve-cells."

General Properties of the Spinal Cord.

In treating of the functions of the spinal cord, we shall consider, first, its general properties, as shown by direct stimulation of its substance in different situations; next, its functions as a conductor; and, finally, its action as a nerve-centre.

The first indication that the different columns of the cord were possessed of different properties is to be found in the experiments of Magendie. This observer, however, was somewhat indefinite in his conclusions, particularly with regard to the anterior columns; but he stated distinctly that the posterior columns are sensitive: "If we lay bare the cord in any portion of its extent, and if we touch, or prick slightly posteriorly, the two fasciculi situated between the posterior roots, the animal gives signs of exquisite sensibility; if, on the other hand, we make the same trials upon the anterior portion, the evidences of sensibility are scarcely apparent." Since this time, numerous observers have experimented upon the different columns, both on the surface and in the deep portions of the cord, with varying results. These observations we do not propose to discuss fully in detail, but shall refer simply to certain of them, made within a few years with the advantage of a knowledge of the reflex phenomena following irritation of the cord, which must always be taken into consideration in such experiments.

In 1861, Chauveau, as the result of numerous experiments performed upon horses, cows, sheep, goats, rabbits, pigs, dogs, and cats, stated that the antero-lateral columns of the cord were inexcitable, both on the surface and in the deep portions. The facts upon which this assertion was based were, that direct stimulation of these portions of the cord in living animals, whether by mechanical means or by feeble galvanic shocks, produced no contraction of muscles and no pain. Upon irritating the posterior columns, either by mechanical or galvanic stimulus, Chauveau noted pain and reflex movements when the irritation was applied to the surface, but the results were negative when the deep portions of the columns were operated upon. The surface of the posterior columns seemed to possess the same general properties as the posterior roots of the nerves, especially near the roots, where the sensibility was most marked, gradually diminishing in intensity toward the median line; but the deep portions of the cord were everywhere found completely insensible and inexcitable.

The experiments and conclusions of Chauveau have a most important bearing upon the physiology of the cord, and they are opposed to the views of the majority of physiological writers, although they have been admitted by some experimenters. We shall discuss first the experiments upon the antero-lateral columns, which are most remarkable in their negative results. We shall use the term excitability as signifying the property of the cord which enables it to conduct a stimulus applied directly to it to certain muscles, producing convulsive movements confined to these muscles, and not of a reflex character. We shall apply the term sensibility to the property by virtue of which an irritation directly applied is conveyed to the brain and produces a painful impression.

The experiments of Chauveau and some others upon the antero-lateral columns are simply negative; but their results are directly opposed to those of numerous experimenters, who have produced local and restricted convulsive movements by direct irritation of both the superficial and the deep portions of these columns.

With regard to the posterior columns, the views of Chauveau are in advance of those of previous observers, only in so far as he has shown that, although the surface of this portion of the cord is endowed with sensibility, its deeper portions are entirely insensible, except in the immediate proximity of the posterior roots of the nerves.

In view of the importance of the question under consideration, and of the contradictory results of experiments, we repeated, in 1863, the experiments of Chauveau, under conditions as nearly physiological as possible. We had often had occasion to note the diminished sensibility of the roots of the spinal nerves immediately following the very severe operation of opening the spinal canal, and had also noted that the sensibility increased, probably approaching the normal standard, after the animal had been allowed a few hours of repose. For this reason, we made our observations about two hours after the first operation. To avoid the suspicion of an extension of the galvanic current beyond the portion of the cord which we desired to stimulate, the irritation was first made by simply scratching the parts with the point of a needle. The following experiment is the type of several, in all of which the results were identical:

May 28, 1863, at 1 P. M., the laminæ and the spinous processes of the three lower lumbar vertebræ were removed from a medium-sized dog. There was no very great hæmorrhage. The spinal cord and the roots of three of the nerves were exposed, and the wound was then closed. The operation was performed with the animal under the influence of ether, and it lasted about three-quarters of an hour.

About two hours after the first operation, the animal was brought before the class at the Long Island College Hospital. The wound was opened, and the properties of the anterior and posterior roots were demonstrated. The following observations were then made upon the spinal cord:

The external surface of the posterior columns was irritated by scratching with the point of a needle. This produced pain, the more marked the nearer the irritation was brought to the origin of the posterior roots. The surface of the cord was almost insensible at the median line. A feeble galvanic stimulus was then applied by means of a *pince électrique*, with the same results. The deep portions of the posterior columns were then irritated, but without effect.

The cord was then divided transversely, and mechanical and galvanic stimulus were applied to the cut surfaces.

The surface of the upper end of the cord was irritated with the needle, and the needle was plunged deeply into its substance, without effect. The same negative results followed application of the galvanic stimulus.

The lower end of the cord was then elevated with a hook, and the surface of the anterior columns was irritated by the needle and by galvanism. The invariable effect was convulsive movements in the lower extremities, without pain. The same irritation was applied to the deep portions of the anterior columns with like results; viz., convulsive movements in the lower extremities, following the irritation immediately.

The above-mentioned phenomena were fully verified by repeated experiments, and the animal was then killed by section of the medulla oblongata.

The general movements accompanied by evidences of pain were readily distinguishable from the local convulsive movements with no pain.

This experiment fully confirms the observations of Chauveau with regard to the posterior columns, but it shows, in opposition to Chauveau, that the anterior columns are excitable, both at the surface and in the deep portions. The recent observations of Vulpian are also opposed to the results obtained by Chauveau with regard to the antero-lateral columns. From a number of carefully-executed experiments, Vulpian draws the following conclusions:

"1. The gray substance is absolutely inexcitable.

"2. The anterior fasciculi possess a certain degree of motor excitability.

"3. There is no doubt that the posterior fasciculi are very excitable. They are sensitive and excito-motor if the cord be left intact, and simply excito-motor if the cord be divided transversely and separated from the encephalon. It is the same, but to a less degree, in that portion of the lateral fasciculi contiguous to the posterior fasciculi."

In the face of definite and positive experiments showing the excitability of certain portions of the cord, it is impossible to accept the purely negative results obtained by Chauveau and others.

As the result of the most definite and reliable experiments of others, bearing upon the question of the properties of the cord, and of our own observations, we have arrived at the following conclusions:

The gray substance is probably inexcitable and insensible under direct stimulation.

The antero-lateral columns are insensible, but are excitable both on the surface and in their substance; and direct stimulation of these columns produces convulsive movements in certain muscles, which movements are not reflex and are not attended with pain. The lateral columns are less excitable than the anterior columns.

The surface, at least, of the posterior columns is very sensitive, especially near the posterior roots of the nerves. The deep portions of the posterior columns are probably insensible, except very near the origin of the nerves.

The above conclusions refer only to the general properties of different portions of the cord, as shown by direct stimulation, in the same way that we demonstrate the general properties of the nerves in their course. In all probability, the fibres in the white and gray substance of the central nervous system conduct motor stimulus from the brain and sensory impressions to the brain, while they themselves may be insensible and inexcitable under direct stimulation.

Transmission of Motor Stimulus in the Cord.—The antero-lateral columns of the cord, in both the white and the gray substance, are entirely insensible to direct irritation, and they conduct the motor stimulus from the centres to the periphery. This statement may be accepted, as the result of positive demonstration, with very little qualification. If the posterior columns of the cord be divided or even removed for a certain length, the animal retains the power of voluntary motion intact. On the other hand, if the antero-lateral columns of the cord be divided on both sides, the power of voluntary motion is lost absolutely in all parts supplied with nerves coming from the cord below the section. It would be an interesting point to determine positively the relative importance of the white and the gray substance of the anterior columns in the transmission of motor stimulus; but this has thus far been impossible. We cannot with certainty divide the gray matter of the anterior columns completely and leave the white substance intact, nor can we divide the white substance without injuring the gray. As far as experiments go, however, they seem to show that transmission is not effected exclusively by the white substance, but that the gray matter plays an important part in this function. We shall refer farther on to the action of the gray substance in the transmission of sensory impressions.

It is evident, from anatomical facts as well as from the results of direct experimentation, that the fibres of conduction of the motor stimulus pass from the brain to the anterior roots of the nerves, through the spinal cord, from above downward, and that there is no other medium for the transmission of the will to the muscles. Wherever the cord be divided, all the muscles supplied by nerves given off below the section are paralyzed. From the brachial enlargement of the cord, nerves of motion pass to the superior extremities, and the inferior extremities are supplied mainly by nerves coming from the lumbar enlargement. The direction of these motor fibres in the cord itself has been elucidated only by experiments upon living animals. If the anterior columns alone be divided in the dorsal region, there is almost complete paralysis of the lower extremities. If the lateral columns be divided in this situation, without injuring the anterior columns, voluntary movements of the lower extremities are diminished but are not abolished. If the anterior columns be divided high up in the cervical region, there is a diminution in the voluntary movements, but this is by no means so marked as when the section is made in the dorsal region; but, if the lateral columns be divided in the upper cervical region, the paralysis is almost or quite complete. These facts clearly show that the situation of the chief motor conductors of the cord is different in the dorsal and in the cervical region. In the dorsal region, while conduction of the motor stimulus takes place through fibres contained both in the anterior and in the lateral columns, the transmission is mainly through the anterior columns, the lateral columns being much less important. In the cervical region, the conditions are reversed, and the conduction takes place chiefly by means of the lateral columns. Passing from above downward, therefore, the motor fibres are situated, in the cervical region, mainly in the lateral columns; but progressively, as they pass through the dorsal and the lumbar portions of the cord, these fibres change their location and are found chiefly in the anterior columns.

Recent observations have not sustained the old idea that the lateral columns of the cord contain fibres which preside specially over the movements of the thorax. The experiments of Vulpian upon this point are conclusive. If the lateral column be divided upon one side at about the third or fourth cervical vertebra, there is considerable enfeeblement of the muscles of the thorax upon the corresponding side, but there is also partial loss of power in the limbs, which is more marked in the anterior extremity. This diminution in power in the thoracic muscles is such that, in ordinary tranquil respiration, the side corresponding to the section does not move; but, in difficult respiration or in crying, the movements are very marked.

Decussation of the Motor Conductors of the Cord.—Well-established anatomical and pathological facts show conclusively that there is a complete decussation of the motor conductors of the cord; so that the stimulus of volition generated in one lateral half of the brain always passes to the opposite half of the body. If a lesion occur in the brain upon one side, so as to produce total paralysis of motion, the opposite side of the body is paralyzed, while voluntary motion is absolutely intact on the side corresponding to the injury. In the anterior pyramids of the medulla oblongata, the decussation of the fibres is easily demonstrated anatomically. In view of these facts, concerning which there is no difference of opinion, it only remains to show by physiological experiments that decussation actually takes place at the medulla oblongata, and to submit to the same method of inquiry the following important question: Assuming that crossing of motor fibres takes place at the medulla, is this the sole seat of decussation of these fibres, or does it also take place in certain portions of the cord below?

The question of decussation at the medulla oblongata is easily answered. In the first place, we have the crossed action in hemiplegia and the easy anatomical demonstration of the decussating fibres. The experimental confirmation of these facts is not so simple, for the reason that animals survive operations upon the medulla oblongata for a very short time. As far as can be learned, however, from the latter mode of inquiry, the conclusions drawn from anatomy and pathology are fully sustained. If the medulla be exposed in a living animal, and "if a section is made longitudinally just at the place of the decussation of the anterior pyramids, so as to divide completely all of the decussating elements, we find that, although the animal lives some time after the operation, it has no voluntary movement at all in any of the limbs, which are almost always the seat of convulsions." (Brown-Séquard.)

The question of decussation of motor fibres in the cord itself is one which can be settled only by physiological experiments, as the course of the decussating fibres, if they exist, cannot be demonstrated anatomically. It is remarkable that Galen submitted this point to experimental investigation, by dividing the cord longitudinally in the median line in the lumbar region. This operation was not followed by loss of voluntary power in the lower extremities, showing that the motor fibres do not cross the median line, at least in this portion of the cord. Recent experiments upon the cervical portions of the cord show that there is a very slight decussation of motor fibres in this situation. The first observations pointing to this conclusion are those of Brown-Séquard. "There is always, even in mammals, after a transversal section of the whole or a lateral half of the spinal cord, at least some appearance of voluntary movements in the side of the injury, and always also a diminution of voluntary movements in the opposite side; so that, in animals, there seems to be in the spinal cord a decussation of a few of the voluntary motor conductors. As there seems to be no such decussation in man, at least according to several pathological facts, we shall not insist upon its existence in animals."

Van Kempen has repeated and extended the very remarkable experiment of Galen, with the most satisfactory results. This observer made a median, longitudinal section of the cord in dogs and rabbits, at the site of the fifth, sixth, and seventh cervical vertebræ. "This experiment was followed by partial paralysis of voluntary movements in the posterior extremities, so that the animal thus operated upon moved the posterior limbs and was able to change his position, without, however, being able to raise himself."

As there is some difference in the results of observations upon different animals, and as decussating motor fibres have never been demonstrated in man, it is impossible to apply the above experiments without reserve to the human subject; but they show, nevertheless, that, in mammals, the motor columns of the cord probably do not decussate in the dorso-lumbar region; that partial decussation occurs in the cervical region; and that the decussation is completed in the anterior pyramids of the medulla oblongata.

Transmission of Sensory Impressions in the Cord.—Early in the physiological history of this portion of the nervous system, Longet made a number of experiments, which seemed to show that the posterior columns of the cord were the conductors of sensory impressions to the brain, and that the antero-lateral columns transmitted the motor stimulus. These were made by applying a stimulus directly to the cord itself. Longet discredited observations made by dividing different portions of the cord, for the reason that he supposed that the mere operation of exposing the cord and of removing the dura mater was followed by a depression of the nervous action sufficient to render the evidences of sensibility in the lower extremities scarcely appreciable. The conclusions drawn from these experiments were at first accepted by nearly all physiological writers, and it was generally admitted that the transmission of sensory impressions was effected solely by the posterior columns. It was found that the gray matter of the cord was both insensible and inexcitable, and the conduction was supposed to take place exclusively through the white substance. The views of Longet, however, were in direct opposition to those of Bellingeri, who claimed, in 1823, to have demonstrated by experiment, that sensory impressions were conveyed to the brain exclusively by the gray substance of the cord, and that sensibility persisted in the lower extremities after complete section of the posterior white columns.

At the time the above-mentioned experiments were made, our knowledge of the properties of the cord was very incomplete, and it was difficult to understand how any of its fibres could conduct sensory impressions and yet be insensible to direct stimulation; but now we know that the gray matter does act as a conductor, and yet it is certainly insensible. The simple questions now to be determined are the following:

1. Does or does not the white substance of the posterior columns of the cord conduct sensory impressions to the brain?

2. Does the entire gray substance of the cord act as a conductor of sensation?

3. Do both the gray matter of the cord and the white substance of the posterior columns act as conductors, or does either one act to the exclusion of the other?

These questions may now be considered as definitively answered by the most positive and unmistakable results of experiments upon living animals, which, while they render the precise function of the white substance of the posterior columns to a certain extent a matter of conjecture, leave no doubt with regard to the parts of the cord which act as conductors of sensory impressions.

The experimental answer to the first question is capable of but one construction. If the white substance of both posterior columns be divided, the sensibility of the posterior extremities is not diminished, at least as far as can be shown by experiments upon animals, in which these points are always difficult of determination. On the other hand, if every portion of the cord be divided except the posterior white columns, sensibility is completely lost in the parts below the section. The accuracy of these results cannot be called in question, especially when controlled by experiments showing the conducting properties of the gray substance of the cord; and they show that, whatever may be the functions of the posterior white columns, they do not serve as conductors of sensory impressions.

The second question admits of an equally positive answer from the results of experimental inquiry. If the entire substance of the cord, except the posterior columns of white matter, be divided transversely, as we have just seen, sensibility is abolished in all parts below the section; but, as we have stated in treating of the transmission of motor stimulus by the cord, voluntary motion is also destroyed. Experiments show, farthermore, that sensory impressions are conveyed exclusively by the gray substance. "If the anterior, the lateral, and the posterior columns of the spinal cord are divided transversely, at the dorsal region, one set at one place, another at a distance of one or two inches, and the third also at the same distance from the second, so that the only channel of communication between the posterior limbs and the sensorium is the gray matter, of which, however, several parts have, unavoidably, been divided (such as the anterior and the posterior gray cornua, and also more or less of the central gray matter), we find that the posterior limbs are still sensitive, though evidently less than in the normal condition." (Brown-Séquard.)

It is impossible to divide the gray matter of the cord alone, without injuring, more or less, the white substance; but, when the gray matter is divided with very slight injury of the white substance, sensibility in the parts below the point of section is totally destroyed. As regards the part of the gray substance specially concerned in the transmission of sensory impressions, the results of experimental investigation have not been so definite; but Brown-Séquard is of the opinion that the transmission takes place chiefly in the gray matter surrounding the central canal, while it may also occur to some extent in other portions.

The answer to the third question is deduced from the answers to the first two. The gray matter and the white substance of the cord do not participate in the transmission of sensory impressions, this being effected by the gray substance, especially its central portion, to the exclusion of the white.

The precise office of the posterior white columns of the cord is still a matter of conjecture. If these parts be insensible, except on the surface and near the posterior roots of the nerves, and if they take no part in the transmission of sensory impressions to the brain (which seems to have been conclusively proven), what is their function?

The anatomical relations of the posterior white columns, the results of experiments upon living animals, and certain well-marked pathological phenomena, point very strongly to a connection between these columns and the coördination of muscular movements.

Probable Function of the Cord in Connection with Muscular Coördination.—Anatomists have not been able to trace satisfactorily the direction of all of the fibres contained in the posterior columns; but it is probable that at least some of these fibres serve as longitudinal commissures, and connect together the nerve-cells, extending for a greater or less distance both upward and downward in the cord. This anatomical arrangement is rendered probable chiefly by the results of experiments.

If the posterior columns be completely divided, by two or three sections made at intervals of from three-fourths of an inch to an inch and a quarter, the most prominent effect is a remarkable trouble in locomotion, consisting in a want of proper coördination of movements.

In the remarkable disease known under the name of locomotor ataxia, there is a very peculiar condition of the muscular system, in which, while the power of the muscles is but slightly diminished, the movements of progression show great deficiency in coördinating power, frequently attended with more or less disturbance in the sensibility of the parts affected. These symptoms are associated with structural disease of the cord, generally limited to the posterior columns and the posterior roots of the spinal nerves.

Many years ago, before locomotor ataxia had been generally recognized by pathologists, Todd made the following remarkable statement with regard to the posterior columns: "I have long been impressed with the opinion, that the office of the posterior columns of the spinal cord is very different from any yet assigned to them. They may be in part commissural between the several segments of the cord, serving to unite them and harmonize them in their various actions, and in part subservient to the function of the cerebellum in regulating and coördinating the movements necessary for perfect locomotion." Todd farther states that this view is supported by the phenomena observed in cases of disease "distinguished by a diminution or total loss of the power of coördinating movements. . . . In two examples of this variety of paralysis, I ventured to predict disease of the posterior columns, the diagnosis being founded upon the views of their functions which I now advocate; and this was found to exist on post-mortem inspection; and in looking through the accounts of recorded cases in which the posterior columns were the seat of lesion, all seemed to have commenced by evincing more or less disturbance of the locomotive powers, sensation being affected only when the morbid change of structure extended to and more or less involved the posterior roots of the spinal nerves."

It is only necessary to add that the views of Todd have been in the main confirmed in the numerous cases of locomotor ataxia that have lately been so fully described by pathologists; and, from these facts, it is more than probable that the posterior columns contain fibres connecting the different segments of the cord, and that they play an important part in the coördination of muscular movements. The general function of coördination will be considered more fully in connection with the cerebellum.

Decussation of the Sensory Conductors of the Cord.—In hemiplegia due to injury of the brain, the paralysis occurs upon the side of the body opposite to the cerebral lesion. The phenomenon ordinarily observed is simply paralysis of motion; but in those cases, however, in which both motion and sensation are abolished upon one side of the body, the lesion in the brain is also found to be upon the opposite side. It is evident, therefore, that there is a decussation of the conductors of sensory impressions as well as of the conductors of the motor stimulus.

As early as 1822, Fodéra made a longitudinal section of the spinal cord in the lumbar region, exactly in the median line. In this experiment, "sensation was destroyed, and in part motion upon the two sides." Inasmuch as in this section it is only possible to divide the fibres passing from one lateral half of the cord to the other, it is evident that the sensory conductors must decussate in the spinal cord itself. As far as we know, this is the first experiment pointing to the decussation of sensory fibres in the cord, the observations of Galen, to which we have already referred, being limited to the phenomena of motion.

The next experiments bearing upon the decussation of the sensory conductors in the cord are those of Van Deen. Among the numerous observations made upon the spinal cord by this physiologist, are one or two in which he noted the fact that, after section of one lateral half of the cord in the frog, at the site to the third dorsal vertebra, "the animal had no real loss of sensibility in the posterior extremity on the side on which the half of the spinal cord had been cut." Although Van Deen did not distinctly state, as a conclusion drawn from these observations, that there is decussation of the sensory conductors in the cord, the fact of section of one lateral half of the cord with no loss of sensation on the corresponding side of the body remains as one of the first experimental arguments in favor of the crossed action.

Experiments upon living animals as well as pathological facts show that, after section or injury confined to one lateral half of the cord, the general sensibility upon the corresponding side of the body is very much exaggerated, producing a condition of well-marked hyperæsthesia. This remarkable fact was distinctly noted by Fodéra, in 1822. This observation has been confirmed, and the experiments very much extended, by Brown-Séquard. Cases presenting the same phenomena have also been observed in the human subject, when one side of the cord has been invaded by disease.

Physiologists are at a loss to explain the hyperæsthesia which follows section of the sensory conductors of the cord, but the fact nevertheless remains. The exaggeration of sensibility is not due to section of certain fibres, which might be supposed to increase the impressibility of the remaining fibres, for, as was shown by Vulpian, it is sufficient to prick with a pin one of the lateral halves of the cord to observe these remarkable phenomena. With these few words, we shall leave the subject of hyperæsthesia from injury to the cord, and pass to the crossed action of its sensory conductors.

In treating of the cord as a conductor of sensory impressions, we have already shown that this function is performed by the gray substance alone. We have also seen, in connection with the phenomena of conduction of the motor stimulus, that this is effected by the antero-lateral columns, which do not act as sensory conductors, except by virtue of their gray matter. As it is impossible to divide the gray matter with certainty without injuring the white substance, and, as we are fully acquainted with the motor properties of the cord, we are prepared to comprehend the effects upon conduction of sensory impressions which follow division of one or the other lateral half. In our detail of experiments, we shall not consider the phenomena of hyperæsthesia, but confine ourselves to the loss or diminution of sensibility.

Brown-Séquard was the first to demonstrate decussation of the sensory conductors in the cord itself; and, although his experiments upon this subject are almost innumerable, and his writings, scattered, voluminous, and sometimes not free from the obscurity due to unnecessary refinement and elaborateness of detail, the main facts can be expressed in a very few words; and he may justly be said to have created the physiology of the sensory conductors.

Brown-Séquard repeated the experiments of Galen and of Fodéra, dividing the cord longitudinally in the median line, producing complete paralysis of sensation upon both sides in all the parts below the section. By this operation, if the section had been made accurately in the median line, the only fibres that could be divided were those passing from one side of the cord to the other.

The second experimental proof of the decussation of sensory fibres consists in transverse section of one or the other of the lateral halves of the cord. If one lateral half of the cord be divided, sensibility is abolished in the parts below the section, upon the opposite side of the body. In an article published in 1858, Brown-Séquard details very succinctly an experiment showing this fact, though his first experiments were made in 1849. He denuded the cord in the lumbar region in a vigorous dog, and made sections upon one side, progressively deeper and deeper, from without inward. When the section included about one-third of the lateral half, the sensibility seemed slightly augmented upon the opposite side. This section involved only a part of the lateral white column and a small portion of the anterior cornu of gray matter. When the section was extended so as to involve about two-thirds of the lateral half, the sensibility was notably diminished upon the opposite side. When the section extended to the median line, the sensibility was very much diminished; and, when it extended just beyond the median line, it was entirely abolished upon the opposite side. These observations, and others of the same nature, show conclusively that, in the animals experimented upon at least, there is a decussation of the greatest part of the sensory conductors in the cord itself.

The course of the fibres in their decussation is indicated by farther experiments, which show that the sensitive fibres from the posterior roots of the nerves "pass along the posterior columns only a little way, and leave them to enter the central gray matter." It is undoubtedly in this gray substance that they pass from one side to the other, probably through the cell-prolongations. The fact that the fibres pass in the cord a short distance before they decussate, and that they pass downward as well as upward, is well shown by the following experiment:

"If we divide transversely a lateral half of the spinal cord in two places, so as to have three pairs of nerves between the two sections, we find that the middle pair has almost the same degree of sensibility as if nothing had been done to the spinal cord, while the two other pairs have a diminished sensibility, the upper one particularly in its upper roots, and the lower one in its lower roots; which facts seem to show that the ascending fibres of the upper pair, and the descending fibres of the lower one, have been divided before they had made their decussation.

"If there is only one pair of nerves between two sections, its sensibility is almost entirely lost, as then the transversal fibres are almost alone uninjured (most of the ascending and descending being divided), which fibres are employed for reflex action, and hardly for the transmission of sensitive impressions." (Brown-Séquard.)

The experimental facts just cited conclusively show decussation of sensory conductors in the cord in the animals operated upon; and this has been sufficiently confirmed by other experimenters to render the fact certain. It is possible that the crossed action may not be so complete in some other classes of animals, which would account for the results obtained by those who have denied decussation; but cases of disease of the cord in the human subject all go to show that the crossed action is complete in man.

Summary of the Action of the Spinal Cord as a Conductor.

The antero-lateral columns of the cord, comprising that portion included between the anterior median fissure and the origin of the posterior roots of the nerves, are insensible to direct irritation, and serve as conductors of the motor stimulus from the brain to the anterior roots of the nerves. If these columns be divided, voluntary motion is lost in all parts below the section. If the rest of the cord be divided, leaving the antero-lateral columns intact, the power of voluntary motion remains. Throughout the greater part of the cord, this action is direct, and division of the antero-lateral columns upon one side produces paralysis of motion upon the corresponding side of the body. There is a decussation of the motor fibres at the medulla oblongata, and probably a partial decussation in the cord itself in the upper cervical region. In the dorsal region and below, the motor conducting fibres are situated chiefly in the anterior columns; but, in the cervical region, these fibres pass to the sides and are contained chiefly in the lateral columns. The conduction of motor stimulus is probably not effected exclusively by the white substance, but is transmitted in part by the gray matter.

The gray substance of the cord serves as the medium of transmission of sensory impressions to the brain. This is effected chiefly by the gray matter surrounding the central canal, but it may take place to some extent in other portions. If the entire gray matter be divided, with but slight injury to the white substance, sensation is lost in all parts situated below the section. The white substance does not conduct sensory impressions to the brain, either in the antero-lateral or the posterior columns. The most probable function of the white substance of the posterior columns is to unite the different segments of the cord together by longitudinal commissural fibres; and this portion of the cord has an important influence in coördinating the muscular movements.

The sensitive nerve-fibres from the posterior roots of the spinal nerves pass in the cord for a short distance upward and downward. They then penetrate the gray matter and decussate throughout the entire length of the cord. Division of one lateral half of the cord is followed by complete paralysis of motion upon the corresponding side of the body in all parts below the section, by anæsthesia in all parts below the section, upon the opposite side of the body, and by hyperæsthesia in the parts below the section, upon the corresponding side of the body.

The anatomical points bearing upon the physiological action of the cord are the following:

The fibres from the anterior roots penetrate the anterior gray cornua directly and are in immediate connection with the prolongations of the motor cells. The motor cells also have prolongations which pass to the brain in the white substance. The motor fibres are thus directly connected with the cellular structures in the cord (the elements probably concerned in reflex movements) and the cells are in connection with conducting fibres to the brain.

The fibres from the posterior roots take several directions. Some of them pass to the gray substance. A portion passes to the posterior columns, some extending upward and others downward. The decussation, which is rendered certain by physiological experiments, has not been satisfactorily followed by anatomists. It undoubtedly takes place chiefly in the gray substance, probably in part by a crossing of the fibres themselves, and in part by a crossing of prolongations from the cells with which certain fibres from the posterior roots are connected.

Action of the Spinal Cord as a Nerve-Centre.

It has long been known that decapitation of animals does not immediately arrest muscular action; and the movements observed after this mutilation present a certain degree of regularity, and, of late years, have been shown to be in accordance with well-defined laws. Under these conditions, the regulation of such movements is effected through the spinal cord and the nerves connected with it. If an animal be decapitated, leaving only the cord and its nerves, there is no sensation, for the parts capable of appreciating sensation are absent; nor are there any true voluntary movements, as the organ of the will is destroyed. Still, in decapitated animals, the sensory nerves are for a time capable of conducting impressions, and the motor nerves can transmit a stimulus to the muscles; but the only part capable of receiving an impression or of generating a motor stimulus is the gray matter of the cord. If, in addition to the removal of all of the encephalic ganglia, the cord itself be destroyed, all movements of voluntary muscles are abolished, except as they may be produced by direct stimulation of the muscular tissue or of individual motor nerves.

We must regard the gray matter of the brain and spinal cord as a connected chain of ganglia, capable of receiving impressions through the sensory nerves and of generating the so-called nerve-force. The great cerebro-spinal axis, taken as a whole, has this general function; but some parts have separate and distinct properties and can act independently of the others. The cord, regarded as a conductor, connects the brain with the parts to which the spinal nerves are distributed. If the cord be separated from the brain in a living animal, it may act as a centre, independently of the brain; but the encephalon has no communication with the parts supplied with nerves from the cord, and it can only act upon the parts which receive nerves from the brain itself.

It has been pretty clearly shown that, when the cord is separated from the encephalon, an impression made upon the general sensory nerves is conveyed to its gray substance, and is transformed, as it were, into a stimulus, which is transmitted to the voluntary muscles, giving rise to certain movements, independently of sensation and volition. This impression is said to be reflected back from the cord through the motor nerves; and the movements occurring under these conditions are called reflex. As they are movements excited by stimulation of sensory nerves, they are sometimes called excito-motor.

The term reflex may properly be applied to any generation of nerve-force which occurs as a consequence of an impression received by a nerve-centre; and reflex phenomena are by no means confined to the action of the spinal cord. The movements of the iris are reflex, and yet they take place in many instances without the intervention of the cord. The movements of respiration are reflex, and these are presided over by the medulla oblongata. Movements of the intestines and the involuntary muscles generally are reflex, and they involve the action of the sympathetic system of nerves. Impressions made upon the nerves of special sense, as those of smell, sight, hearing, etc., give rise to certain trains of thought. These involve the action of the brain, but still they are reflex. In this last example of reflex action, it is sometimes difficult to connect the operations of the mind with external impressions as an exciting cause; but it is evident, from a little reflection, that this is often the case. This fact is illustrated by operations of the brain which take place, as it were, without consciousness, as in dreams. It has been clearly shown that a particular direction may be given to the thoughts during sleep, by impressions made upon the sense of hearing. A person sleeping may be made to dream of certain things, as a consequence of hearing peculiar noises. Examples of this kind of mental reflex action are sufficiently numerous and well-authenticated.

From the above considerations, it is evident that the term reflex may be properly used in connection with many phenomena involving the action of the sympathetic system and of the brain; but it is generally understood as applying especially to involuntary movements, occurring without consciousness, as the result of impressions made upon the afferent nerves and involving the independent action of the spinal cord.

Reflex Action of the Spinal Cord.—In 1832 and 1833, Marshall Hall described minutely the movements which take place in decapitated animals as a consequence of stimulation of the sensory nerves, and he formularized these phenomena under the head of "the reflex function of the medulla oblongata and medulla spinalis." Since this publication, a new interest has been attached to the writings of some of the older physiologists, in which reflex action, as it is now understood, had been mentioned more or less definitely. In the history of important advances in physiological knowledge, it has often been the case that discoveries have been foreshadowed by the earlier writers; and bibliographical research shows that the literature of the cord as a nerve-centre forms no exception to this, which is almost the rule. Some of the allusions to the cord as a centre of reflex action, made anterior to 1833, are vague and indefinite; but, on the other hand, certain excito-motor actions were very accurately described by Legallois, as early as 1812. Marshall Hall grouped and classified these phenomena and showed their relations to the cord as an independent centre; but he has no claim to the title of the discoverer of reflex action, and his experiments themselves presented little that was really new.

The experiments of Marshall Hall, published in 1832 and 1833, are familiar to every physiologist, as supplying nearly all of the omissions of previous observers. The points which he assumed to have experimentally demonstrated by his researches are the following: A decapitated animal, the only part of the cerebro-spinal axis which remains being the spinal cord, will make no movements, if completely protected from all external impressions. An impression made upon the sensory nerves of a decapitated animal is reflected by the cord, through the motor nerves, to the muscles, and gives rise to reflex movements. If the cord be destroyed, no movements follow stimulation of the surface. If the centripetal and the centrifugal nerves be divided, no reflex movements can take place. Experiments upon decapitated animals accord with the results of observations upon acephalous fœtuses and in cases of complete paraplegia from injury to the cord. All of the involuntary movements observed in the healthy body are explained by the theory of reflex action. These observations of Marshall Hall were, in the main, confirmed by Müller, in the year succeeding their first publication; and, by some writers, the credit of the discovery of the mechanism of reflex action is given to both Müller and Marshall Hall.

From the point of view which the present condition of science enables us to take with regard to the reflex action of the cord, we have to determine the accuracy of the observations of Marshall Hall, and to follow out the advances that have been made by more recent observers. It is important, as the first step in our inquiry, to ascertain the exact condition of decapitated animals as regards their capacity for muscular movements; and upon this point there is some difference of opinion. Marshall Hall thought that an animal (a frog, for example) after decapitation, was incapable of any voluntary movement, or of any movement which did not have, for its exciting cause, an external impression. We take the example of frogs, because these are the animals most commonly used by experimenters.

All who have experimented upon frogs have seen them jump about vigorously after decapitation; and the question whether these be spontaneous movements, so called, or an excito-motor action, is more difficult to determine than would at first sight appear. It would be unphilosophical to assume that, because the animal has been decapitated, the movements are due to external impressions only, if we use this as evidence against the possibility of spontaneous movements under these conditions. The obvious necessity of the argument is to remove all possibility of external impressions or of irritation of the cord itself. Upon this point, we can only speak positively from our own experiments. If a frog be decapitated, so as to leave only the spinal cord intact, if we wait for from one to three minutes until the effects of the shock and local irritation have subsided, if we then, when the animal has become perfectly quiet, cover it with a bell-glass, and finally, if we remove all possibility of jarring the table on which the animal is placed, there is no movement of muscles. In making an experiment of this kind, we occasionally see movements which are due to a very feeble impression, such as a breath of air or a jar from the street, but which is perfectly evident to the observer; and, when a movement is once made, this gives rise to another impression, and thus, successive actions of the muscles may take place. The movements in jumping are so simple that they seem, sometimes under these conditions, to be voluntary. The effect of feeble excitations is also very marked in animals poisoned with strychnine; but, even here, we do not have movements unless an impression be first made upon the sensory nerves. When we come to experiments upon the mammalia, there can hardly be any question of this kind; for here, as the rule, no movements are observed after the encephalic ganglia have been removed, unless the sensory nerves be pretty strongly stimulated. Analogous phenomena are observed in the lower extremities, in cases of paraplegia in the human subject.

The next important question to determine is with regard to the nature of movements excited by external stimulation in decapitated animals, especially frogs; for some of these movements are so regular as to appear to be connected with sensation and volition. The experiments of Pflüger upon this point are very remarkable. These have been repeatedly confirmed, and there can be no doubt with regard to their accuracy. Pflüger carefully removed from a frog the entire encephalon, leaving only the spinal cord. He then touched the surface of the thigh over the inner condyle with acetic acid, to the irritation of which frogs are peculiarly sensitive. The animal thereupon rubbed the irritated surface with the foot of the same side, apparently appreciating the locality of the irritation, and endeavoring, by a voluntary effort, to remove it. The foot of this side was then amputated, and the irritation was renewed in the same place. The animal made an ineffectual effort to reach the spot with the amputated member, and, failing in this, after some general movements of the limbs, rubbed the spot with the foot of the opposite side. Although this experiment does not always progress precisely in the manner described, it has succeeded perfectly in so many instances as to lead some physiologists to conclude that sensation and volition are not entirely abolished by removal of the encephalon, at least in frogs.

The remarkable phenomena just detailed are to be regarded from two points of view: first, with reference to their bearing upon the question of the existence of perception and volition in the spinal cord of the frog; and second, the question of the application of these phenomena to the physiology of the cord in man and the higher classes of animals. The conditions of the experiment in the frog are simply these: Instead of exposing the surface to a single and instantaneous stimulation, the excito-motor effects of which are observed as a direct response to the irritation and immediately cease, we have, by the application of acetic acid to the surface, a prolonged impression upon the sensory nerves, which, by virtue of the anatomical connections between the different parts of the cord, is probably dispersed throughout the entire spinal axis. That powerful impressions may be thus dispersed, there can be no doubt, as we shall see farther on. The phenomena under consideration certainly point to an appreciation by the cord of the locality of a powerful impression, and this could be manifested in an animal only by an apparent muscular effort to reach the irritated spot; but we can hardly reason from this fact that, in man and the higher animals, the spinal cord shares with the brain the power of appreciating what we know as sensation and of generating the stimulus of true voluntary movement. If a sudden and very powerful painful impression be made upon the surface in man under normal conditions, the hand may be instantly applied to the affected part, apparently before we really appreciate the pain or have time to make a distinct effort of the will; but the connections between the different parts of the cerebro-spinal axis do not permit us to isolate the action of the cord. Certain it is that, in the higher animals, after removal of the encephalon, and in experiments upon decapitated criminals and patients suffering from paraplegia, there is no evidence of true sensation or volition in the spinal cord; and, in man and the higher animals, we must regard all muscular movements which depend solely upon the action of the cord as a nerve-centre as automatic and entirely independent of consciousness and of the will.

It is easy to determine, by experiments to which we have already incidentally alluded, that the muscular movements dependent upon nervous action, occurring in decapitated animals, are due to the action of the spinal cord as a nerve-centre. In an animal in which the reflex phenomena are very marked, as they are after decapitation, especially if the animal be poisoned with strychnine or opium, all movements immediately cease when the cord is destroyed. That the gray matter of the cord is the part concerned as a centre in the production of these phenomena, is probable, in view of what we know with regard to the general functions and properties of this substance; and experiments have shown that this is the fact. If, in a decapitated frog, we make an incomplete longitudinal section of the cord in the median line, leaving only a slight communication between the two sides, we may sometimes succeed, by strongly irritating the skin of one leg, in producing reflex movements, not only in the same leg, but in the leg of the opposite side; and it is reasonable to suppose that the irritation is propagated from one side to the other through the cells of the gray matter.

The conditions essential to the manifestations of reflex phenomena depending upon the action of the cord are very simple and easily understood.

In the first place, it is necessary that one or more of the posterior roots of the spinal nerves should be in communication with the cord, in order to conduct the impression to this nerve-centre. If all of the posterior roots be divided, there is no nervous communication between the periphery and the centre, and no movements follow irritation of the surface. When the excitability of the cord is exaggerated, as in poisoning by strychnine, a single posterior root is sufficient to conduct an impression to the cord, which will give rise to violent contractions of all the muscles. This is due to a dispersion of the impression, under these conditions of increased excitability, from the single point of entrance of the posterior root, throughout the cord. In animals that have been simply decapitated, a similar diffusion of impressions may also take place. If a comparatively feeble single impression be made upon any part of the general surface, as the rule, the subjacent muscles only are the seat of contraction; but, if the impression be more powerful, or if it be prolonged, as when we apply a drop of acetic acid to any part of the skin of a frog, this impression may be diffused throughout the cord, producing contractions of the general muscular system. We have already shown, in treating of the general properties of the sensory nerves, that an impression made at any point in the course of a nerve is conducted to the centre. Reflex movements may, consequently, be produced by stimulating the sensory nerves in their course or by irritating the posterior roots of the spinal nerves.

We have already stated that the cord must retain its anatomical integrity, in order to receive an impression made upon the centripetal nerves and transform it, as it were, into a stimulus, which is reflected back by the motor nerves and produces muscular contraction. It is also evident that the motor nerves must retain their connection with the cord and be in a condition to conduct the stimulus reflected by the cord to the muscles.

The reflex excitability of the spinal cord is increased to a marked degree by separating this portion of the cerebro-spinal axis from the encephalon, and the same is true for the lower portion of the cord, when a section is made in the dorsal or lumbar region. It is difficult to find an entirely satisfactory explanation of this fact; and the phenomena observed under these conditions are, in this regard, like the exaggerated sensibility of portions of the general surface after section of certain columns of the cord.

In experiments upon the lower animals, the reflex phenomena are greatly exaggerated in intensity in the tetanic condition observed in poisoning by opium or strychnine. Take, for example, a frog decapitated and poisoned with strychnine. No reflex movements occur unless an impression be made upon the sensory nerves; but the slightest irritation, such as a breath of air or a slight jar, throws the entire muscular system into a condition of violent tetanic spasm. The same phenomena are observed in cases of poisoning by strychnine or of tetanus in the human subject. This fact is important in its relations to the treatment of these conditions; for it is evident that, in such cases, the exhaustion due to the violent spasms may be moderated by carefully avoiding all unnecessary irritation of the surface.

FIG. 224.—*Frog poisoned with strychnine.* (Liégeois.)

It was shown a number of years ago, that the inhalation of anæsthetic agents may abolish all of the ordinary reflex phenomena. Whether this be due to an action upon the cord itself or to a paralysis of the sensory nerves, it is difficult to determine. Ordinarily, in animals rendered insensible by anæsthetics, the reflex acts of respiration continue; but these may also be arrested, as has been observed by all who have experimented with anæsthetics, especially with chloroform. A common way of determining that an animal is completely under the influence of ether is by an absence of the reflex act of closing the eyelids when the cornea is touched.

It now only remains to show that the phenomena of reflex action observed in experiments upon the inferior animals, especially frogs, are applicable to the human subject, and to indicate the muscular actions which depend upon the cord as a nerve-centre.

It is only necessary, after what has gone before, to indicate in a general way the phenomena observed in the human subject which illustrate the reflex action of the cord. It is a common observation, in cases of paraplegia in which the lower portion of the cord is intact, that movements of the limbs follow titillation of the soles of the feet, these movements taking place independently of the consciousness or the will of the subject experimented upon. Acephalous fœtuses will present general reflex movements and movements of respiration, and will even suck when the finger is introduced into the mouth. Observations of this kind are so numerous and familiar that they need not be cited in detail. Experiments have also been made upon criminals after decapitation; and, although the reflex phenomena are not so well marked and cannot be excited so long after death as in cold-blooded animals, they are sufficiently distinct.

It is difficult, in studying, in the human subject, the ordinary phenomena of movements in the voluntary muscular system, to isolate the reflex phenomena from those acts involving sensation and volition. In many persons, titillation of the soles of the feet produces violent contractions of muscles, which cannot be arrested by an effort of the will, and this may even be followed by general convulsions. When we unexpectedly touch an irritating surface with the hand, the muscles of the arm act so quickly that we may suppose that this takes place before we really appreciate the painful sensation, and, if the impression be very severe, we may have movements more or less general; in operating upon highly-sensitive parts, it is frequently impossible to arrest reflex movements, as the closing of the eyelids when the cornea is touched; true reflex movements may be produced by carefully-executed experiments upon persons asleep; we cannot arrest the act of vomiting induced by titillation of the fauces; and other instances of this kind might be cited.

Most of the true involuntary movements are reflex; but these have been or will be considered under their proper heads. The movements of deglutition depend upon an impression made upon the mucous membrane of the pharynx, etc. The movements of respiration are excited by an impression made upon the general sensory nerves, due to want of oxygen, as we have shown in treating of respiration. The ejaculation of semen is also reflex. Important reflex actions take place through the sympathetic nerves, such as the movements of the intestines, vaso-motor movements, etc.; but these will be considered fully under the head of the sympathetic system. Secretion, the action of the heart, the contractions of the uterus, the action of the sphincters, the movements of the iris, etc., are regulated by the sympathetic and the cerebro-spinal system.

As regards the farther action of the cord as a nerve-centre, there are undoubtedly many functions which are influenced more or less by this portion of the cerebro-spinal axis; but these have been treated of under their appropriate heads or will be considered hereafter.

CHAPTER XXI.

THE ENCEPHALIC GANGLIA.

Physiological divisions of the encephalon—Weight of different parts of the brain and of the entire encephalon—Some points in the physiological anatomy of the encephalon and its connections—The cerebrum—General properties of the cerebrum—Functions of the cerebrum—Extirpation of the cerebrum in the lower animals—Pathological facts bearing upon the functions of the cerebrum—Comparative development of the cerebrum in the lower animals—Development of the cerebrum in different races of men and in different individuals—Location of the faculty of articulate language in a restricted portion of the anterior cerebral lobes—The cerebellum—Some points in the physiological anatomy of the cerebellum—Course of the fibres in the cerebellum—General properties of the cerebellum—Functions of the cerebellum—Extirpation of the cerebellum in animals—Pathological facts bearing upon the functions of the cerebellum—Connection of the cerebellum with the generative function—Development of the cerebellum in the lower animals—Ganglia at the base of the encephalon—Corpora striata—Optic thalami—Tubercula quadrigemina, or optic lobes—Ganglion of the tuber annulare—Medulla oblongata—Physiological anatomy of the medulla oblongata—Functions of the medulla oblongata—Connection of the medulla oblongata with respiration—Vital point—Connection of the medulla oblongata with various reflex acts—Rolling and turning movements following injury of certain parts of the encephalon—General properties of the peduncles.

The anatomy of the encephalon is so complex, that it can be treated of with advantage only by a very minute and carefully-illustrated description, such as is to be found in some of the elaborate anatomical works or in special treatises upon the nervous system. We shall not consider under a distinct head the general physiological anatomy of the brain, for the reason just given, and also because we are as yet ignorant of the exact connection between the structure and arrangement of many of its parts and their physiology. We know that the gray substance is capable of appreciating general and special impressions received by the peripheral nervous system, and of generating the so-called nerve-force. Impressions are conveyed to this portion of the cerebro-spinal axis by the sensory conductors, passing to the brain, either through the cord or by the cranial nerves, and by the nerves of special sense, as well as those of general sensibility. The stimulus which gives rise to voluntary movements is generated in the brain and is conveyed by the motor nerves to the appropriate muscles. We have seen, also, that the centres of the encephalon may be concerned in reflex action. In addition, parts of the brain act as centres of sensation and volition and are concerned in the varied phenomena of intellection.

The encephalon, or what is ordinarily known as the brain, consists of a number of ganglia, or collections of gray matter, connected with each other, and also, by the different columns of the cord, with the motor and sensory nerves of the general system. Certain of these ganglia have separate and distinct functions which are more or less completely understood; while there are, in addition, masses of gray substance, the physiological relations of which are as yet obscure or entirely unknown. The greatest and the most important of all, the gray matter of the cerebral hemispheres, undoubtedly has subdivisions connected with distinct attributes of the mind; but our positive knowledge with regard to these divisions is, at the present day, very meagre, although this subject has long been a favorite field for philosophical speculation.

Confining ourselves strictly to the limits of positive information, we may recognize the following parts of the encephalon as distinct ganglia: 1. The gray matter of the cerebral hemispheres; 2. The gray matter of the cerebellum; 3. The olfactory ganglia; 4. The gray matter of the corpora striata; 5. The gray matter of the optic thalami; 6. The tubercula quadrigemina; 7. The gray matter of the tuber annulare, or pons Varolii; 8. The ganglion of the medulla oblongata. In addition, the following parts have been made the subject of physiological investigation or speculation, with results more or less

FIG. 225.—*Vertical section of the encephalon.* (Hirschfeld.)

1, *medulla oblongata*; 2, *tuber annulare*; 3, *cerebral peduncle*; 4, *cerebellum*; 5, aqueduct of Sylvius; 6, valve of Vieussens; 7, *tubercula quadrigemina*; 8, *pineal gland*; 9, *inferior peduncle*; 10, *superior peduncle*; 11, middle portion of the great cerebral fissure; 12, *optic thalamus*; 13, 13, gray commissure; 14, choroid plexus; 15, infundibulum; 16, *pituitary body*; 17, tuber cinereum; 18, bulb of the fornix; 19, anterior perforated space; 20, root of the motor oculi communis; 21, optic nerve; 22, anterior commissure of the cerebrum; 23, foramen of Monro; 24, section of the fornix; 25, *septum lucidum*; 26, 27, 28, *corpus callosum*; 29, 30, 31, 32, 33, 34, *convolutions and sulci of the cerebrum*. The olfactory ganglia and corpora striata are not shown in this section.

definite: The peduncles of the cerebrum and of the cerebellum; the pineal gland; the corpus callosum; the septum lucidum; the cerebral ventricles; and the pituitary body. We have, however, little if any positive information concerning these parts, except as regards their general anatomical relations; and their physiology really amounts to little more than a history of the vague speculations of the ancients or the fruitless experiments of modern observers. It is to be hoped that future anatomical investigations, chiefly in following out the course of the fibres of the encephalon and their connections with the cells of the different collections of gray matter, will throw light upon the functions of this part of the cerebro-spinal axis; but, at present, all physiologists will admit that we have received very little aid from this source. In our anatomical descriptions, therefore, we shall confine ourselves to those points that are strictly physiological.

Weight of different Parts of the Brain and of the entire Encephalon.—Most of the tables of the weight of the healthy adult brain of the Caucasian, given by different observers, show essentially the same results, the differences amounting to only one or two ounces for the entire encephalon. The average given by Quain is 49½ ounces, avoirdupois, for the male, and 44 ounces for the female. This is the general result obtained by combining the tables published by Sims, Clendinning, Tiedemann, and Reid. The number of male brains weighed was 278, and of female brains, 191. In males, the minimum weight was 34 ounces, and the maximum, 65 ounces. In 170 cases out of the 278, the weight ranged from 46 to 53 ounces, which may be taken as the general average. In females, the minimum was 31 ounces, and the maximum, 56 ounces. In 125 cases out of the 191, the weight ranged from 41 to 47 ounces.

Quain assumes, from various researches, that, in new-born infants, the brain weighs 11·65 ounces, for the male, and 10 ounces, for the female. In both sexes, "the weight of the brain generally increases rapidly up to the seventh year, then more slowly to between sixteen and twenty, and again more slowly to between thirty-one and forty, at which time it reaches its maximum point. Beyond that period, there appears a slow but progressive diminution in weight of about one ounce during each subsequent decennial period; thus confirming the opinion, that the brain diminishes in advanced life."

The comparative weights of the several parts of the encephalon, calculated from observations upon the brains of fifty-three males and thirty-four females, between the ages of twenty-five and fifty-five, are as follows:

Divisions of the encephalon.	Males.	Females.
Average weight of the cerebrum	43·98 oz.	38·75 oz.
Average weight of the cerebellum	5·25 "	4·76 "
Average weight of the pons and medulla oblongata	0·98 "	1·01 "
Average weight of the entire encephalon	50·21 oz.	44·52 oz.

The proportionate weight of the cerebellum to that of the cerebrum, in the male, is as 1 to $8\frac{4}{7}$, and in the female, as 1 to $8\frac{1}{4}$.

The specific gravity of the whole encephalon is about 1036, that of the gray matter being 1034, and of the white, 1040.

The above weights are quoted from Quain's admirable work upon anatomy, and the normal range of variations and averages only are given. When we come to treat of the cerebrum and its relations to intelligence, we shall discuss the weights of the brain in idiots and in persons of extraordinary intellectual power, as far as any data upon these points are to be found.

Some Points in the Physiological Anatomy of the Encephalon and its Connections.—The direction of the fibres in the encephalon, their connections with the cells of the gray substance, the course of commissural fibres connecting together the different parts of the gray substance of the cerebrum, the cerebellum, and the deeper ganglia, and finally the avenues of communication between the fibres of the encephalon and the cord, are points of exceeding intricacy; and many of them are still so uncertain and obscure, that they cannot as yet be connected satisfactorily with the exact results of physiological inquiry. All that we can do at present, is to recognize certain ganglionic masses, the separate functions of which have been more or less accurately defined, and to show, as far as possible, their anatomical relations to each other and to the spinal cord.

The separate collections of gray matter concerning which we possess positive physiological knowledge are, the gray matter of the cerebral hemispheres and of the cerebellum, the corpora striata, optic thalami, tuber annulare, or pons, and the medulla oblongata. To these may be added, the olfactory ganglia, which preside over the sense of smell, and the tubercula quadrigemina, or optic lobes, which are the centres connected with vision. The minute anatomy of the nerve-fibres and the nerve-cells, with their mode of connection with each other, have been already considered with sufficient minuteness under the head of the general structure of the nervous system. We shall here discuss chiefly the direction of the fibres through which the encephalic ganglia are connected with the periphery, the fibres connecting the different ganglia with each other, and, in the case of the larger ganglia, certain commissural fibres connecting together their different parts.

In the wealth of literature pertaining to the minute anatomy of the encephalon, it is somewhat difficult to separate and define the well-established facts which have a direct bearing upon physiology. Perhaps the most elaborate and, to a certain extent, the most satisfactory observations upon the various points to be considered, are those of Luys; but this author describes the course of the fibres with an exactitude that seems hardly justified, in all instances, by the facts, in view of the inevitable difficulty and uncertainty of some of the processes employed; and the graphic and admirable delineations by which the work is illustrated, though professedly schematic, present a degree of ideality which inspires some distrust with regard to the accuracy of the general conclusions. According to Luys, the fibres of the encephalon have several directions, as follows:

The gray matter of the cerebral hemispheres, as we shall see farther on, is composed of a mass of nerve-cells, connected together by their prolongations into a plexus, which, in its turn, is connected with the fibres of the white substance. From this cortical cellular plexus, white fibres arise, which may be divided, according to their direction and destination, into two classes: The first class consists of curved commissural fibres, which pass into the white substance to a certain depth and return to the gray matter, connecting thus the gray substance of adjacent convolutions. The existence of these fibres and their direction are well established. The second class consists of fibres which, arising from the gray substance of the convolutions, connect these with the corpora striata and the optic thalami. These may be called the converging fibres; and their general direction, as far as it has been ascertained, is as follows:

FIG. 226.—*Diagrammatic representation of the direction of the fibres in the cerebrum.* (Le Bon.)

Arising from the internal, concave surface of the cortical substance of the cerebrum, the converging fibres, at first running side by side with the curved commissural fibres, separate from the latter as they curve backward to pass again to the cortical substance, and are directed toward the corpora striata and the optic thalami. The limits of the irregular planes of separation of the commissural and the converging fibres contribute to form the boundaries of the ventricular cavities of the brain. If we study the course of the converging fibres arising from all points in the concave surface of the cerebral gray matter, we find that they take various directions. The fibres from the anterior region of the cerebrum pass backward and form distinct fasciculi which converge to the gray substance of the corpora striata. The fibres from the middle portion converge regularly to the middle region of the external portions of the optic thalami. The fibres from the posterior portion pass from behind forward and distribute themselves in the posterior portion of the optic thalami. The fibres from the convolutions of the hippocampi and the fascia dentata are lost in the gray substance lining the internal borders of the optic thalami. In addition to these converging fibres and the curved commissural fibres connecting the different convolutions of each hemisphere with each other, are commissural fibres which connect the two hemispheres, as well as fibres connecting together the corpora striata and the optic thalami of the two sides.

Certain of the fibres converging from the gray substance of the hemispheres to the corpora striata and optic thalami are probably connected with the cells in the gray matter of these parts. Other fibres pass through the corpora striata and optic thalami to become finally connected with the fibres of the medulla oblongata, and, through the medulla oblongata, with the columns of the spinal cord. Following the antero-lateral columns of the cord from below upward, they ascend to the medulla oblongata, decussate in the median line, and pass from the medulla to the brain. Certain of these ascending fibres, which are nearly all continuations of the antero-lateral columns of the cord, ascend to the brain by passing deeply through the pons Varolii; other fibres ascend in the cerebral peduncles, or crura cerebri; and other fibres pass to the tubercula quadrigemina. As the bundles of fibres ascend from the medulla oblongata, they become more and more numerous by reënforcements of fibres, probably derived from the cells of the collections of gray matter in their course.

We have attempted, in the above sketch of the fibres of the brain, to give a succinct account of the points that are most interesting from their physiological relations, and to confine our description, as far as possible, to anatomical facts that have been definitively settled and are now generally accepted. But, as we have before remarked, the course of the fibres and their connections are so exceedingly intricate, that we cannot rely entirely upon purely anatomical investigations. The results obtained by anatomists should be controlled, as far as possible, by physiological and pathological observations. When anatomical researches are directly opposed to the conclusions to be deduced from experiments upon living animals, in view of the great uncertainty of the former, it will generally be reasonable to assume that they are erroneous or incomplete. We know, as the results of experiments upon animals, that the motor stimulus is conducted from the brain by the antero-lateral columns of the cord, and that the conducting fibres decussate at the medulla oblongata. This fact has been verified by pathological observations, chiefly in cases of injury to the brain-substance from hæmorrhage, softening, etc. We know that impressions are appreciated as sensations in some part of the cerebrum, and that the sensory conductors also decussate; as is shown by occasional paralysis of both motion and sensation as a consequence of brain-lesions. It is evident, therefore, that sensory conductors pass to the brain, but their precise course is not easy to determine. We have seen, in treating of the action of the cord as a conductor, that sensory impressions are transmitted by the gray substance alone, and it is probably through connections between the cells of the different centres that these impressions are finally carried to the brain. The physiological fact of the conduction of sensory impressions is fully confirmed by pathology, but its mechanism has been very little if at all elucidated by anatomical researches.

We have remaining certain anatomical points relating to the cerebrum, cerebellum, tuber annulare, and medulla oblongata, to be described separately in connection with these divisions of the encephalon.

The Cerebrum.

The anatomical description which we have just given of the encephalon will answer for most of the points of physiological interest connected with the cerebrum. As we have seen, the cerebrum constitutes more than four-fifths of the encephalic mass. Its gray matter, which is external and follows the convolutions, is from $\frac{1}{12}$ to $\frac{1}{8}$ of an inch in thickness. Writers have described this substance as existing in several layers, but this division is mainly artificial. In certain parts, however, particularly in the posterior portion of the cerebrum, the gray substance is quite distinctly divided into two layers, by a very delicate intermediate layer of a whitish color.

There is a marked difference in the appearance of the cells in the most superficial and in the deepest portions of the gray substance. The superficial cells are small and present a net-work of delicate, anastomosing fibres, resembling the cells of the posterior cornua of the gray substance of the cord; while the deepest cells are large and resemble the so-called motor cells of the cord. Between these two extremes, in the intermediate layers, there is a gradual transition in the size of the cells. This anatomical fact points to the possibility of distinct functions of the cells belonging to the superficial and the deep layers; viz., that the larger cells are for the generation of the motor stimulus, while the smaller are for the reception of sensory impressions. This, however, is a mere supposition, incapable, as yet, of positive demonstration.

The mode of connection between the cellular and the fibrous elements of the nervous system has already been considered and does not demand farther mention. We shall also pass over the amorphous matter, nuclei, myelocytes, etc., found in the central nervous matter, as these points possess little or no physiological interest.

General Properties of the Cerebrum.—By the general properties of the cerebrum, we mean the effect, or the absence of effect, observed when the gray or white substance is subjected to direct irritation. While some of the older writers state that the brain is both irritable and sensible, nearly all authorities, up to a very recent date, have been agreed that direct stimulation of the white or the gray substance of the greatest part of the brain produces neither pain nor convulsive movements. In numerous experiments upon pigeons, we have invariably noted complete insensibility and inexcitability of both the gray and the white substance of the cerebral hemispheres. The generally-accepted view has been that a great part of the substance of the cerebrum is neither excitable nor sensible, in the sense in which these terms are applied to the ordinary mixed nerves. There can be no doubt with regard to the conducting properties of the white matter of the brain, but the nerve-fibres here seem to conduct impressions conveyed to them by the sensory nerves and the stimulus generated by the nerve-cells, without being capable of receiving or conducting artificial impressions applied directly to their substance.

We have said that a great part of the cerebral substance seems to be neither excitable nor sensible to direct stimulation; but we must make an exception in favor of certain portions of the cerebrum, which have lately been shown to possess excitability, their action being confined to particular sets of muscles. In 1870, Fritsch and Hitzig, exposing the cerebral hemispheres in dogs, found that certain parts of its anterior portion responded to a feeble galvanic current. Each galvanization produced movements restricted to particular sets of muscles; but it was difficult to say whether the contractions were due to stimulation of the white or of the gray substance. Different centres for the sets of muscles were accurately determined. The centre for the muscles of the neck was located in the middle of the frontal convolution; external to that, was a centre for the extensor and adductor muscles of the forelegs; and so on, other centres for sets of muscles being found in the anterior portion of the hemispheres. By passing an interrupted current through these parts, tetanus of particular muscles was produced. In other observations, when the gray substance was removed at the points mentioned, there was partial loss of power, but not paralysis, of the sets of muscles corresponding to the centres operated upon. The authors regarded this as due to a loss of "muscular sense." In these experiments the action was always crossed. It was also found that, after severe hæmorrhage, the excitability of the cerebrum quickly disappeared, which may account for the negative results obtained by previous experimenters. No motor properties were discovered in the posterior portion of the cerebrum.

The experiments just cited throw a new light upon the properties of the cerebral substance. It has always been found difficult to experiment upon the great encephalic centres without disturbing the physiological conditions so seriously as to render the results of direct observations of this kind more or less indefinite. Now that it is ascertained that, in all probability, these centres readily lose their normal properties, as a simple consequence of hæmorrhage and exposure of the parts, we are less disposed to accept the older experiments, in which the cerebral tissue was apparently shown to be incapable of receiving direct artificial impressions.

Since the first publication of the remarkable experiments to which we have just referred, the question of the excitability of certain parts of the cerebral hemispheres has attracted a great deal of attention and has been made the subject of numerous experiments. The most notable of the later observations on this subject are those of Ferrier, of London, by whom the original experiments of Fritsch and Hitzig have been fully confirmed. Although the methods employed by Ferrier were less delicate and accurate than those of the German observers, the results obtained are of great value. Many other physiologists have since confirmed the essential points developed in the original investigations; and the only serious objection to the results is the possibility of diffusion of the galvanic current to recognized motor tracts. This question is pretty well settled by the following experiment made by Dr. Putnam, of Boston: Having localized experimentally a distinct motor centre on the surface of the brain, he made a flap, about one-twelfth of an inch thick, by a section parallel to the surface of the brain and involving this centre. With the flap *in situ*, the current which had before excited muscular contraction had no effect. It is evident that the section of the brain-substance would necessarily cut off the physiological conduction of a stimulus; but, with the flap *in situ*, the section would probably not interfere with the diffusion of the galvanic current itself.

In the present condition of the question, the above is all that it seems necessary to say, in a systematic work upon physiology, concerning the excitable centres of the cerebrum. That these excitable centres exist, there can be little doubt; and the idea that the movements produced by their galvanization are reflex is not justified by experimental facts. These observations have been confirmed by Hitzig as late as in 1874; and his last experiments fully substantiate the views advanced in his first paper, showing loss of power in certain muscles, following destruction of portions of the brain-substance corresponding to the excitable points.

Functions of the Cerebrum.

The history of the functions of the encephalon belongs without question to physiology and is one of the most extensive and interesting of the subdivisions of the science; but its range is so extensive, that it has long been regarded as a science by itself and is only treated of exhaustively in special treatises upon psychology. The study of psychology has been pursued by the method of observation much more than by direct experiment. It comprehends, it is true, the facts deduced from experiments upon living animals, but the results obtained by this method are comparatively few and their scope is restricted. Nevertheless, they are sufficiently definite; and, if these results be corrected and applied to the human subject by a comparison with pathological facts, there still remains in psychology much that may be regarded as within the range of experimental physiology; for pathological cases are very frequently available to the physiologist as accidental experiments indicating the functions of parts of the human organism. We cannot restrict ourselves, however, to this method in the study of the intellectual phenomena; and we must draw upon facts in comparative anatomy and physiology, anthropology, and, finally, upon the direct observation and classification of the intellectual processes.

The experimental physiologist has shown that the encephalon may receive impressions and appreciate them as sensations; that impressions may be here connected and give rise to various of the phenomena of animal and intellectual existence; that impressions are recorded by the memory; and, finally, that certain parts are endowed with special functions. But beyond this, psychology is a science mainly of introspective observation, the facts contributed by the experimentalist being few and barren. The observer of intellectual phenomena studies the process of development of the mind; he soon separates the instinctive phenomena, observed in the lower animals and in the human being without experience, from the acts which follow experience, observation, the recording of impressions by memory, and the generation of ideas; he brings his perfected intelligence to bear upon the process of development of the same kind of intelligence in the human being progressing from infancy to adult life; and, finally, the psychological philosopher attempts, by introspective observation, to study the workings of the perfect intellect, his only means of investigation being the very intelligence he is endeavoring to comprehend.

At the present day, we are in possession of a sufficient number of positive facts to render it certain that there is and can be no intelligence without brain-substance; that, when brain-substance exists in a normal condition, intellectual phenomena are manifested, with a vigor proportionate to the amount of matter existing; that destruction of brain-substance produces loss of intellectual power; and, finally, that exercise of the intellectual faculties involves a physiological destruction of nervous substance, necessitating regeneration by nutrition, here, as in other tissues in the living organism. The brain is not, strictly speaking, the organ of the mind, for this statement would imply that the mind exists as a force, independently of the brain; but the mind is produced by the brain-substance; and intellectual force, if we may term the intellect a force, can be produced only by the transmutation of a certain amount of matter. In view of these facts, which have long been more or less fully recognized, though not, perhaps, very accurately defined in words until within a few years, it is not surprising that attempts have been made to locate the different mental attributes in particular portions of the brain. The pseudo-science of phrenology is the most marked example of such an attempt; but this has so slight a basis in fact, that it does not, at the present day, merit serious scientific discussion.

In treating of the functions of the cerebrum, we shall not discuss psychology, except in so far as physiologists have been able to connect the mind, taken as a whole, with a distinct division of the nervous system. In this we shall draw upon experiments on living animals, facts in comparative physiology, in pathology, and, to a certain extent, the relations clearly shown to exist between the development of intelligence and certain of the nerve-centres, in different races of men and different individuals. With regard to the location of particular functions in distinct portions of the cerebrum, we have but little definite knowledge, beyond the experiments already cited in treating of the irritability of the cerebral substance, and the probable location of the faculty of speech. The latter point will be fully discussed in its appropriate place.

Extirpation of the Cerebrum in the lower Animals.—It is, perhaps, sufficiently evident, from anthropological and pathological observations as well as the study of comparative physiology, that the intellectual faculties reside in the encephalon; but these methods of investigation do not clearly indicate the special functions of different parts of the cranial contents. We have seen, in our general sketch of the anatomy of the brain, that this is by no means a simple organ, and that certain parts, although they are bound together by commissural fibres, have sufficient anatomical distinctness to lead the physiologist to suppose that they may have separate and peculiar properties and functions. One of the most valuable methods of investigation of the functions of these separate ganglia is that of extirpation of one or more, leaving the others, as far as possible, intact. This method was first employed with marked success by Flourens and has since been adopted by numerous experimenters. It must be remembered, however, that there is no subject of physiological inquiry in which it is so difficult to apply experiments upon the inferior animals to the human subject, and none in which the results of experiments should be received with greater caution. The reason for this is apparent enough. The brain and the intellectual power of man are so far superior to the development of this organ and its properties in the lower animals, that some philosophers have regarded the human intelligence as distinct in nature as well as in amount. Although we are by no means prepared to accept this proposition, regarding, as we must, the intelligence of man as simply superior in development to that of the lower animals, it is evident that this difference in the degree of development is so enormous as to render the human mind hardly comparable with the intellectual attributes of animals low in the scale. But, when the human brain is slightly developed, as in idiots, or when the intellectual faculties are simply diminished in activity, as in certain cases of disease, the being is reduced to a condition very like that of some of the lower animals.

Experiments upon different classes of animals show clearly that the brain is less important, as regards the ordinary manifestations of animal life, in proportion as its relative development is smaller. For example: if we remove the cerebral hemispheres in fishes or reptiles, the movements which we call voluntary may be but little affected; while, if the same mutilation be performed in birds or some of the mammalia, the diminished power of voluntary motion is much more marked. It would be plainly unphilosophical to assume, because a fish or a frog will swim in water and execute movements after removal of the hemispheres very like those of the uninjured animal, that the feeble intelligence possessed by these animals is not destroyed by the operation. It is not only possible, but probable, that, in the very lowest of the vertebrates, the functions of the nervous centres are not the same as in higher animals. There is, for example, a fish (the lancet-fish, *Amphioxus lanceolatus*), that has no brain, all of the functions of animal life being regulated by the gray substance of the spinal cord. It is essential, in endeavoring to apply the results of experiments upon the brain in the lower animals to human physiology, to isolate, as far as possible, the distinct manifestations of intelligence, from automatic movements. Bearing in mind, then, the difficulties of the question and the caution with which all observations upon the great nerve-centres of the lower animals must be received in their applications to pure human physiology, we shall proceed to discuss the phenomena following removal or injury of the cerebrum in direct experiments.

In 1822 and 1823, Flourens communicated to the French Academy of Sciences his remarkable observations upon the different parts composing the encephalon. His experiments are so familiar to physiologists, that it is only necessary here to give his general conclusions. As regards the cerebral hemispheres, he found that the complete removal of these parts in living animals (frogs, pigeons, fowls, mice, moles, cats, and dogs), was invariably followed by stupor, apparent loss of intelligence, and absence even of the ordinary instinctive acts. Animals thus mutilated retained general sensibility and the power of voluntary movements, but were thought to be deprived of the special senses of sight, hearing, smell, and taste. As regards general sensibility and voluntary movements, Flourens was of the opinion that animals deprived of their cerebral lobes possessed sensation, but had lost the power of perception, and that they could execute voluntary movements when an irritation was applied to any part, but had lost the power of making such movements in obedience to a spontaneous effort of the will. One of the most remarkable phenomena observed was entire loss of memory and of the power of connecting ideas. The voluntary muscular system was enfeebled but not paralyzed. Removal of one hemisphere produced, in the higher classes of animals experimented upon, enfeeblement of the muscles upon the opposite side, but the intellectual faculties were in part or entirely retained. Removal of even a considerable portion of both hemispheres was followed by no very marked effect as regards the intelligence.

The observations of Flourens have been repeated by numerous experimentalists and were, in the main, confirmed, except as regards the special senses. Bouillaud, in 1826, made a large number of observations upon pigeons, fowls, rabbits, etc., in which, after removal of the hemispheres, he noted the persistence of the senses of sight and hearing. Longet finally demonstrated the fact that both sight and hearing are retained after extirpation of the hemispheres, even more clearly than Bouillaud, by the following experiments: He removed the hemispheres from a pigeon, the animal surviving the operation eighteen days. When this animal was placed in a dark room and a light was suddenly brought near the eyes, the iris contracted and the animal winked; "but it was remarkable, that when a lighted candle was moved in a circle, and at a sufficient distance, so that there should be no sensation of heat, the pigeon executed an analogous movement of the head." An examination after death showed that the removal of the cerebrum had been complete. An animal deprived of the hemispheres also opened the eyes at the report of a pistol and gave other evidence that the sense of hearing was retained.

With regard to the senses of smell and taste, it is more difficult to determine their presence than to ascertain that the senses of sight and hearing are retained. It is probable, however, that the sense of smell is not abolished, if the hemispheres be carefully removed, leaving the olfactory ganglia intact; and there is no direct evidence that extirpation of the cerebrum affects the sense of taste; indeed, in young cats and dogs, Longet has noted evidences of a disagreeable impression following the introduction of a concentrated solution of colocynth into the mouth, as distinctly as in the same animals under normal conditions.

We shall now proceed to describe, as accurately as possible, the condition of an animal after complete extirpation of the cerebrum, as observed in numerous experiments that we have ourselves made upon this subject, premising the statement that these are merely repetitions of observations made by other physiologists.

A pigeon, in a perfectly normal condition, is deprived of the hemispheres, by removing the calvarium and carefully scooping out the parts with the handle of a scalpel. This operation is usually not difficult, and the hæmorrhage is soon arrested spontaneously. The slit in the scalp is closed with sutures, and the animal is set at liberty. The appearance of the animal after this mutilation is peculiar and characteristic. There immediately supervenes a condition of stupor. There is usually no attempt at movement, and, though the pigeon stands upon its feet, the head is almost buried in the feathers of the neck, the eyes are closed, and the attitude is one of absolute indifference to surrounding conditions. The muscles seem to act with just sufficient vigor to maintain the standing position. If we pinch one of the toes or grasp the beak, there is evident sensation, and a persistent and more or less vigorous effort is made to release the part. It is sufficiently evident, from these and other tests, that sensation and the power of voluntary motion are retained; but, as soon as the animal is left quiet, it relapses into its stupid condition, makes no effort to escape, and apparently loses immediately all recollection of having been disturbed. The irritation has evidently produced a sensation of discomfort and has given rise to a voluntary muscular effort; but there has been no idea of danger, nor an intelligent effort to avoid a repetition of the disagreeable or painful impression.

It is easy to demonstrate, by experiments such as we have just detailed, that the animal sees and hears; but it connects no idea with any thing seen, and the report of a pistol, which, under natural conditions, would excite terror and an idea of danger, simply causes the pigeon to give evidence that the sound has been heard. As we have already stated, it is probable that the animal has the sense of smell, but it is difficult, if not impossible, to establish this point experimentally. The same remark applies to the sensations of hunger and thirst. The animal may feel the want of water and food, but it has no idea of relieving these sensations by drinking and eating, and, if left to itself, will die of inanition.

There has been a great deal of discussion among experimentalists with regard to spontaneous voluntary movements in animals deprived of the cerebral hemispheres. The experimental conditions necessary for determining this point are the following: The observer must be certain that the removal of the hemispheres has been complete; for it has been clearly shown that, even when a small amount of cerebral substance has escaped, the functions of these parts are not entirely abolished. Again, we must be equally certain that movements which seem to be due to a spontaneous act of volition take place when the animal has not been aroused from the condition of stupor which results from the operation. Generally, when the animal is left to itself, the condition of stupor persists; but, when aroused by artificial means, it will walk a few steps, plume the feathers, shake its head, and make various voluntary movements without farther irritation, soon relapsing, however, into somnolency. One of the most accurate and reliable of the recent observers of these phenomena, Vulpian, asserts without reserve, that an animal, deprived completely of the cerebral hemispheres, is incapable of a spontaneous voluntary effort; and we are inclined to an unqualified adoption of this opinion. With regard to a rabbit from which Vulpian had removed the cerebral hemispheres and the corpora striata, he makes the following statement: "I do not hesitate to say that this rabbit is completely deprived of spontaneous volition. All its movements, which are, indeed, much less varied than those of a bird operated upon in the same manner, are exclusively and directly due to a stimulation produced by exterior excitations, or by interior inclinations, such as fatigue, etc."

In view of the very great variety of movements that occur in animals after removal of the cerebrum, it is quite difficult to define precisely what movements are due to voluntary action depending upon some external or interior impression, which are really reflex voluntary movements, and to distinguish them from those which arise from a spontaneous and, perhaps, an intelligent effort of the will. These points have been so admirably described in a recent article, by Onimus, that we quote his concluding summary:

"As a summary, in the inferior animals, as in the superior animals, the removal of the cerebral hemispheres does not cause to disappear any of the movements that previously existed. Only, these movements assume certain peculiar characters. In the first place, they are more regular, they have the true normal type, for no psychical influence intervenes to modify them; the locomotor apparatus is brought into action without interferences, and one could almost say that the *ensemble* of movements is then more normal than in the normal condition.

"In the second place, the movements executed take place inevitably after certain excitations. *It is a necessity* that the frog placed in water should swim, and that the pigeon thrown into the air should fly. The physiologist can then, at will, in an animal without the brain, determine such and such an act, limit it, arrest it; he can anticipate the movements and affirm in advance that they will take place under certain conditions, absolutely as the chemist knows in advance the reactions that he will obtain in mixing certain bodies.

"Another peculiarity in the movements that take place, when the cerebral lobes are removed, is their continuation after a first impression. On the ground, a frog without the brain when irritated makes, in general, two or three jumps at the most; it is rare that it makes but one. Placed in water, it continues the movement of natation until it meets with an obstacle; it is the same in the carp, eel, etc. The pigeon continues to fly, the duck and goose continue to swim, etc. We should say that there is a spring which needs for its action a first impulsion, and which is stopped by the slightest resistance. But, what is striking, is precisely that continuation of the condition once determined, and we cannot refrain from connecting the facts observed in an animal deprived of the cerebral lobes with those which constitute the characteristic properties of inorganic matter. Brought into movement, the animal without a brain retains the movement until there is exhaustion of the conditions of movement, or until it meets with resistance; taken in repose, it remains in the state of inertia until an exterior cause intervenes to bring it out of this condition. It is *living, inert matter*."

There is now no room for discussion with regard to the persistence of general sensibility after removal of the hemispheres. The experiment upon a pigeon leaves no doubt upon this point, but the susceptibility to pain has been much more strikingly illustrated in other animals. Vulpian, in describing the condition of animals operated upon in this way, illustrates the persistence of sensibility in rats and rabbits, by the violent cries which follow painful impressions.

In concluding our consideration of the observations upon inferior animals, it only remains for us to discuss briefly certain late experiments, which have attracted a great deal of attention from the fact that they seem to show that spontaneous volition exists after complete extirpation of the cerebrum. These experiments have been most ably and satisfactorily analyzed by Vulpian. Goltz argues, from experiments upon frogs and the movements executed after extirpation of the brain, that these animals make intelligent muscular efforts when deprived of the hemispheres; and the phenomena observed after this mutilation are indeed very curious. As was shown by Vulpian, in his own experiments, frogs and fishes thrown into water will swim about and the frogs will even succeed in getting out of the water, but then they immediately relapse into a torpid condition. We do not conceive that these facts are in opposition to the statement just made with regard to the absence of spontaneous volition in birds and the mammalia, particularly in view of the slight importance of the functions of the cerebrum as compared with the spinal cord in the lower orders of vertebrate animals. The views lately advanced by Voit are based upon an isolated experiment upon a pigeon that was kept alive for five months after the cerebral lobes had been, as stated by Voit, completely removed. At first the pigeon presented the phenomena usually observed after this operation; but it gradually recovered, until finally it seemed entirely normal, with the single exception that it never would eat, all food being introduced forcibly. Five months after the operation, the pigeon was killed and the encephalic cavity was found filled with a white substance containing dark-bordered nerve-fibres and nerve-cells. Voit never before observed any thing like regeneration of the nervous substance or so complete a restoration of the cerebral functions; and he regarded this as an instance of anatomical and physiological regeneration of the hemispheres. The objections to accepting this observation with the physiological conclusions presented by Voit are, that it is not only possible but probable, that the hemispheres were not entirely removed and that the posterior portion of the encephalon had advanced to occupy in part the space originally filled by the extirpated mass. While we do not assume that anatomical and functional regeneration of the cerebrum in a pigeon is impossible, it must be admitted that such an extraordinary statement as that made by Voit cannot be accepted without reserve, merely upon the basis of a single observation.

Pathological Facts bearing upon the Functions of the Cerebrum.—A careful study of the phenomena which attend certain pathological conditions of the brain in the human subject, such as laceration or pressure from effusion of blood, softening of the nervous substance, etc., taken in connection with the results of experiments upon living animals, throws considerable light upon the functions of certain distinct portions of the encephalon. Cerebral hæmorrhage very commonly involves the corpus striatum, either directly or indirectly, and then we have paralysis of motion limited to the side of the body opposite to the lesion. When the optic thalamus is affected, there is impairment of sensibility upon the opposite half of the body. These facts illustrate the course of the motor and sensory conductors from and to the cerebrum. It is not very common to observe lesions confined to the gray or white substance of the hemispheres, but, when this occurs and when there is no pressure upon the corpora striata or optic thalami, there is no paralysis of motion or sensation, although there may be a certain amount of weakness of the muscles upon the side of the body opposite the injury. Experiments upon the inferior animals have confirmed the conclusions to be drawn from these pathological facts. In frogs, fishes, and birds, when one hemisphere has been removed, the evidences of feebleness of the muscles of the opposite side are not very marked; but they are quite distinct in the adult mammalia.

It is a fact now generally admitted in pathology, that loss of cerebral substance from repeated hæmorrhage is sooner or later followed by impairment of the intellectual faculties. This point it is frequently difficult to determine in a single instance, but an analysis of a sufficient number of cases shows impaired memory, tardy, inaccurate, and feeble connection of ideas, abnormal irritability of temper with a childish susceptibility to petty or imaginary annoyances, easily-excited emotional manifestations, and a variety of phenomena denoting abnormally feeble intellectual power, following any considerable disorganization of cerebral substance. In short, pathological conditions of the brain all go to show that the intellectual faculties are connected with the cerebral hemispheres.

As a final argument drawn from pathology, in favor of the view just stated, we have only to allude to the size of the brain in certain cases of idiocy. There are on record numerous examinations of the brain in idiots, in which this organ has been found to be less than one-half of the ordinary weight; as the cases reported by Tiedemann, of 19¾, 25¼, and 22½ ounces, in three idiots, whose ages were, respectively, sixteen, forty, and fifty years. A case has been reported by Mr. Gore, of an idiotic woman, forty-two years of age, whose brain weighed ten ounces and five grains; and one by Mr. Marshall, of an idiotic boy, twelve years old, whose brain weighed but 8½ ounces. Mr. Bradley, in a late number of the *Journal of Anatomy and Physiology*, gives an elaborate description of the brain of an idiot, thirty-five years of age, extremely emaciated at the time of his death, when he weighed but sixty pounds. The encephalon, including the cerebrum, cerebellum, and pons, weighed twenty-eight ounces, and the proportion of the cerebellum to the cerebrum was as 1 to 5·5. In the healthy adult male of ordinary weight, the encephalon weighs fifty ounces, and the proportion of the cerebellum to the cerebrum is as 1 to 8⅞. Mr. Bradley calls attention to the proportion of the cerebellum to the cerebrum in this case, stating that this is common in the encephalon of idiots. In idiots, the weight of the body is generally much below the normal standard; and, in the case reported by Bradley, the proportionate weight of the encephalon to that of the entire body is even greater than in the healthy adult. If, for example, we double the weight of the body and the brain, we should have, for one hundred and twenty pounds of weight, an encephalon of fifty-six ounces. This point, however, cannot be admitted as an argument against the fact that congenital idiocy is usually attended with an abnormally small development of the hemispheres. Most idiots take little or no exercise; they are under-sized, and have but little muscular vigor; and it is probable that the general development of the body is more or less a consequence of the abnormal cerebral condition. We might compare the weight of the body in Mr. Bradley's case with that of a child from seven to fourteen years of age; and, at this period of life, according to the tables compiled by Quain, the average weight of the encephalon is 45·96 ounces, for the male, and 40·78 ounces, for the female.

The statements just made with regard to the brains of idiots refer to cases characterized by complete absence of intelligence, and farthermore, probably, by very small development of the body. On the other hand, there are instances of idiocy, the body being of ordinary size, in which the weight of the encephalon is little if any below the average. Lélut reports several cases of this kind. In one of these, a deaf-mute idiot, forty-three years of age, a little above the ordinary stature, presenting "idiocy of the lowest degree; no speech; almost no sign of intelligence; no care for cleanliness," the encephalon weighed 48·32 oz. Other cases of idiots of medium stature are given, in which the brain weighed but little less than the normal average. These facts illustrate the difficulty of subordinating individual observations to any general rule, and this is particularly marked with regard to the brain, the structure of which is so complex and difficult of investigation.

Comparative Development of the Cerebrum in the Lower Animals.—It is only necessary to refer very briefly to the development of the cerebrum in the lower animals as compared with the human subject, to show the connection of the hemispheres with intelligence. In man, the cerebrum presents an immense preponderance in weight over other portions of the encephalon; and, in some of the lower animals, the cerebrum is even less in weight than the cerebellum. In man, also, not only the relative but the absolute weight of the brain is greater than in lower animals, with but two exceptions. Todd cites a number of observations made upon the brains of elephants, in which the weights ranged from nine to ten pounds. Rudolphi gives the weight of the encephalon of a whale, seventy-five feet long, as considerably over five pounds. With the exception of these animals, man possesses the largest brain in the zoological scale.

Another interesting point in this connection is the development of cerebral convolutions in certain animals, by which the relative amount of gray matter is increased. In fishes, reptiles, and birds, the surface of the hemispheres is smooth; but, in many mammalia, especially in those remarkable for intelligence, the cerebrum presents a greater or less number of convolutions, as it does in the human subject.

Comparing the relative size of the brain, its complexity of organization, and the increase of its gray substance by convolutions, with the development of intelligence in the animal scale, it is so evident that the cerebrum is the organ presiding over the intellectual faculties, that this point in our argument seems to need no farther discussion.

Development of the Cerebrum in Different Races of Men and in Different Individuals.—It may be stated as a general proposition, that, in the different races of men, the cerebrum is developed in proportion to their intellectual power; and, in different individuals of the same race, the same general rule obtains. Still, this law presents marked exceptions. Certain brains in an inferior race may be larger than the average in the superior race; and it is frequently observed that unusual intellectual vigor is coexistent with a small brain, and the reverse. These exceptions, however, do not take away from the force of the original proposition. As regards races, the rule is found to be invariable, when a sufficient number of observations are analyzed, and the same holds true in comparing a large number of individuals of the same race. Average men have an advantage over average women of about six ounces of cerebral substance; and, while many women are far superior in intellect to many men, such instances are not sufficiently numerous to invalidate the general law, that the greatest amount of intellectual capacity and mental vigor is coincident with the greatest quantity of cerebral substance. If we accept the view, which is in every way reasonable, that the gray substance of the cerebral hemispheres is the generator of the mind, it would be necessary, in comparing different individuals with the view of establishing a definite relation between brain-substance and intelligence, to estimate the amount of gray matter; but it is not easy to see how this can be done with any degree of accuracy.

It is undoubtedly true that proper training and exercise develop and increase the vigor of the intellectual faculties, and that thereby the brain is increased in power, as are the muscles under analogous conditions. This will perhaps explain some of the exceptions above indicated; but an additional explanation may be found in differences in the quality of brain-substance in different individuals, independently of the size of the cerebral hemispheres. One evidence that these differences in the quality of intellectual working matter exist is, that some small brains actually accomplish more and better work than some large brains. This fact may be due to differences in training, to the extraordinary development in some individuals of certain qualities, to intensity and pertinacity of purpose, capacity for persistent labor in certain directions, a fortunate direction of the mental efforts, opportunity and circumstances, etc.; but, aside from these considerations, it is exceedingly probable that there are important individual differences in the quality of generating nervous matter.

In concluding this portion of our argument, we present a table of an exceedingly interesting series of observations upon the comparative weights of the encephalon in the Caucasian, the negro, and the intermediate grades produced by the union of the two races. The observations in this table are hardly sufficient in number to establish the exact relations between the brains in the different grades of color, but they illustrate points of peculiar interest in this country, where the blacks are so numerous and where the union of the two races, white and black, is so common. We also give a list of some of the well-authenticated weights of the encephalon in men whose intellectual faculties had been observed during life. This latter list we have prepared with great care and have introduced some observations not found in most works upon physiology. In estimating the intellectual power of individuals, it is difficult to arrive at exact conclusions, except with regard to men of acknowledged eminence. Still, the statements are as accurate as possible and must be taken for what they are worth. Several of the examples given in this list are marked exceptions to the general rule, that the mental vigor is in proportion to the amount of brain-substance.

We have not considered it necessary to enter into a discussion of the relations of the facial angle to intelligence in the lower animals and in different races of men. It was proposed by Camper to take the angle made at the junction of two lines, one drawn from the most projecting part of the forehead to the alveolæ of the teeth of the upper jaw, and another passing horizontally backward from the lower extremity of the first line, as the facial angle. This angle is, to a certain extent, a measure of the projection of the anterior lobes of the brain. Numerous observations upon the facial angle in different races were made by Camper and by other physiologists and ethnologists. They show, in general terms, that the angle is larger in man than in any of the inferior animals and is largest in those races that possess the greatest development of intellectual power.

Ethnological Table, derived from 405 *Autopsies of White and Negro Brains. Made under the Direction of Surgeon Ira Russell,* 11*th Massachusetts Volunteers.*

	No. of autopsies.	Grade of color.	Average weight of brain.	Maximum weight of brain.	Minimum weight of brain.	Brains 60 oz. and over.	Brains, 55 and under 60 oz.	Brains, 50 and under 55 oz.	Brains, 45 and under 50 oz.	Brains, 40 and under 45 oz.	Brains, 35 and under 40 oz.	Brains less than 35 oz.
	24	White	52·06	64	$44\frac{1}{4}$	1	4	11	7	1	.	.
	25	$\frac{3}{4}$ "	49·05	51	40	1	.	10	12	2	.	.
	47	$\frac{1}{2}$ "	47·07	57	$37\frac{3}{4}$	.	2	13	19	12	1	.
	51	$\frac{1}{4}$ "	46·54	59	$38\frac{1}{2}$	.	2	10	22	11	6	.
	95	$\frac{1}{8}$ "	46·16	57	$34\frac{1}{2}$	.	1	15	50	21	7	1
	22	$\frac{1}{16}$ "	45·18	$50\frac{1}{2}$	40	.	.	3	10	9		.
	141	Black	46·96	56	$35\frac{3}{4}$	.	5	42	51	38	3	.
						2	14	104	171	94	17	1
	405											
Autopsies of Clendinning, Sims, Reid, and Tiedemann,	278	Whites collated from various sources.	$49\frac{1}{2}$	65	34	7	28	99	97	39	7	1

Table of Weights of the Encephalon, in ounces, av., in Individuals, in some of whom the Degree of Intelligence is more or less accurately known.

Cromwell, aged 59 (not accepted by physiologists) .... 82·29 oz.
Byron, aged 36 (not accepted by physiologists) .... 79·00 "
Bricklayer, aged 38; fair intelligence, but could neither read nor write (reported by Dr. James Morris) .... 67·00 "
Cuvier, aged 63 (*Archives générales de médecine*, 1832) .... 64·33 "

Abercrombie, aged 63 (reported by Dr. Adam Hunter)........ 63·00 oz.
Congenital epileptic idiot (reported by Dr. Tuke)........ 60·00 "
Ruloff, aged 53; above medium stature; executed for murder, in 1871; well versed in languages, imagining that he had discovered new and important principles in philology (reported by Dr. George Burr)........ 59·00 "
James Fisk, Jr., aged 37; killed in New York, in 1872; illiterate, but said to possess great executive ability; notorious for colossal and unscrupulous financial speculations (reported by Dr. Marsh)........ 58·00 "
Boy, aged 13; healthy and intelligent; died from injuries caused by a fall (*British Medical Journal*, Oct. 19, 1872)........ 58·00 "
Spurzheim (*Medico-Chirurgical Review*, 1836)........ 55·06 "
Adult man; an idiot since two years of age (Wagner)........ 54·95 "
Laborer, aged 22; died of fracture of the pelvis (Wagner)........ 53·79 "
Daniel Webster, aged 70 (reported by Dr. John Jeffries)........ 53·50 "
Celebrated mathematician, aged 54; above the ordinary stature (Wagner)........ 53·41 "
Agassiz, aged 66 (reported by Dr. M. Wyman)........ 53·40 "
Executed criminal, aged 45; medium stature; of less than ordinary intelligence, and uncultivated (Lélut)........ 53·12 "
Celebrated clinical professor, aged 52; medium stature (Wagner)........ 52·88 "
Mathematician of the first rank, aged 78; medium stature (Wagner)........ 52·62 "
Executed criminal, aged 34; rather large in stature; ordinary intelligence, but singular and somewhat cultivated (Lélut)........ 50·09 "
Dupuytren, aged 58 (Cruveilhier, Husson, and Bouillaud)........ 49·68 "
Day-laborer, aged 49 (Wagner)........ 48·85 "
Executed criminal, aged 29; medium stature; of scarcely ordinary intelligence and uncultivated (Lélut)........ 48·81 "
Executed criminal, aged 42; a little above medium stature; intelligence fine, developed, and slightly cultivated (Lélut)........ 48·81 "
Idiot, of a very low degree of intelligence, aged 37; a little above medium stature; movements very active (Lélut)........ 48·67 "
Deaf-mute, aged 43; a little above medium stature; an idiot, of the lowest degree of intelligence (Lélut)........ 48·32 "
Executed criminal, aged 46; medium stature; of ordinary intelligence, uncultivated, but proud and vivacious (Lélut)........ 48·14 "
Man, slightly imbecile, aged 67; medium stature (Lélut)........ 48·14 "
Man, about 60 years of age (Wagner)........ 48·14 "
Celebrated philologist, aged 54; 5 feet 7½ inches tall (Wagner)........ 47·90 "
Executed criminal, aged 34; small stature; intelligence developed and cultivated (Lélut). 47·79 "
Man, about 24 years of age; died of aortic insufficiency (Wagner)........ 47·69 "
Day-laborer, aged 51 (Wagner)........ 47·44 "
Man, 34 years of age; died of pneumonia (Wagner)........ 47·26 "
Brigand and assassin, aged 32; beheaded (Wagner)........ 46·91 "
Idiot of the lowest degree of intelligence, aged 24; medium stature (Lélut)........ 46·56 "
Executed criminal, aged 27; medium stature; of ordinary and uncultivated intelligence (Lélut)........ 46·21 "
Executed criminal, aged 40; at least of medium stature; intelligence developed and cultivated (Lélut)........ 46·21 "
Railroad laborer, aged 23 (Wagner)........ 46·21 "
Executed criminal, aged 29; intelligence hardly ordinary, and uncultivated (Lélut)........ 45·50 "
Wood-cutter, aged 57; died of vertebral caries (Wagner)........ 44·90 "
Idiot, below the condition of a brute; aged 39 (Lélut)........ 44·30 "
Imbecile, with difficulty in movements; aged 57; intelligence correct, notwithstanding its slight development (Lélut)........ 43·56 "
Man, 34 years of age; died of phthisis (Wagner)........ 43·38 "
Celebrated mineralogist, aged 77; above medium stature (Wagner)........ 43·24 "
Executed criminal, aged 31; small stature; intelligence mobile and exaggerated (Lélut). 42·04 "
Upholsterer, aged 60; died of phthisis (Wagner)........ 40·91 "

Imbecile, aged 23; large stature (Lélut)	38·97 oz.
Idiot, of the lowest degree of intelligence; aged 46; medium stature (Lélut)	36·86 "
Man, 46 years of age; idiocy very profound; very large stature (Lélut)	36·15 "
Man, 44 years of age; idiocy very profound; a little below medium stature (Lélut)	34·39 "

In compiling the foregoing table, we have in every instance consulted the authentic reports of the weights of the brain and have reduced them all to ounces av. with the greatest care. This was found necessary, on account of the important variations in the reports quoted by different physiological authors, especially as regards the brains of Cuvier, Webster, and Dupuytren. We believe that our figures are absolutely correct. The weights of the brains of Cromwell and Byron are given, but there can be hardly any question that the weights are grossly exaggerated. A careful study of the weights given in this table shows the impossibility of applying to individuals an absolute rule that the greatest brain-power is connected with the greatest amount of brain-substance. The men of acknowledged intellectual ability in the table are, Cuvier, Abercrombie, Spurzheim, Webster, Agassiz, Dupuytren, and those cited by Wagner as celebrated mathematicians, professors, etc. A bricklayer, Cuvier, and Abercrombie stand at the head of the list, as regards the weight of the brain; but above Webster and Dupuytren, are Ruloff, Fisk, two idiots, a boy thirteen years old, and a common laborer. Far down in the list, is a celebrated mineralogist, whose brain is at least six ounces below the average. The advanced age of the person referred to (seventy-seven years) would not account for the small weight of the brain, although the weight is undoubtedly diminished in old persons. We are not surprised, then, in the tables based upon observations of thousands of healthy brains of men not remarkable for great intellect, to find many between fifty-five and sixty ounces in weight.

As the general result of all the observations upon the human subject, while we admit that intellectual vigor is in general coincident with large development of the cerebral hemispheres, there are certainly many striking exceptions to this rule when it is applied to individuals.

Location of the Faculty of Articulate Language in a Restricted Portion of the Anterior Cerebral Lobes.—Physiologists are often slow to accept important facts bearing directly upon the functions of parts, drawn exclusively from pathology, especially when these facts are not capable of demonstration by experiments upon the lower animals; and perhaps this is due to a certain distrust of the accuracy of pathological researches as compared with the exact results of well-executed experimental observations. As regards the faculty of speech, however, our study must be confined to man, the only animal capable of articulate language, and our data are drawn exclusively from pathology. Some physiological writers are still disposed to regard the location of the faculty of speech as not definitively settled; but, from a careful study of the pathology of aphasia, we are convinced that there is no point in the physiology of the brain more exactly determined than that the faculty of speech is located in a well-defined and restricted portion of the anterior lobes. This is the more interesting and important, as it is the only sharply-defined faculty that has been accurately located in a distinct portion of the brain.

Aphasia is a pathological condition in which the subject is deprived, more or less completely, of the power of language, spoken or written. This definition includes not alone those cases in which patients are unable to express ideas by speech, but cases in which the idea of language is lost and there is agraphia, or inability to express ideas in writing. Certain cases of this disease present loss of speech because the subject is incapable of coördinating the muscles used in articulation. The patient has a clear idea of language and of the meaning of words and is able to write perfectly well. In other cases, the patient can neither speak nor express ideas in writing. In these, the idea of language is lost. In both of these varieties of the disease, the difficulty is either in the organ presiding over the faculty of speech or in the connections of this organ with the muscles concerned in articulation. Thus regarded, aphasia does not include aphonia from laryngeal disease, or loss of speech such as is observed frequently in hysteria, in the insane, who sometimes refuse to speak from pure obstinacy, or in cases of paralysis of the parts immediately concerned in articulation. The whole history of the disease points to a particular part of the brain, which presides over the faculty of speech.

As a preliminary to the location of the nerve-centre presiding exclusively over speech, it is necessary to establish the existence of the power of articulate language as a distinct faculty; and this is done by cases of disease in which this faculty seems to be lost, the general mental condition being unaffected. Passing over the passages in the writings of the ancients, in which it is stated that the power of speech is sometimes lost, and even some writers in the beginning of the present century, who connected this difficulty with lesions of the anterior lobes of the brain, we come to the observations of Dr. Marc Dax, who, in 1836, read a paper before the medical congress at Montpellier, in which he indicated impairment or loss of speech in one hundred and forty cases of right hemiplegia. Dax concluded, from these observations, that the faculty of articulate language occupies the left anterior lobe of the cerebrum. This memoir, however, attracted but little attention, until 1861, when the discussion was renewed by Broca; and, since then, numerous cases of aphasia with lesion of the left anterior lobe have been reported by various writers. In 1863, M. G. Dax, a son of Marc Dax, limited the lesion to the anterior and middle portion of the left anterior lobe. It was farther stated, by Broca and Hughlings Jackson, to be that portion of the brain nourished by the left middle cerebral artery. According to recent observers, the most frequent lesion in aphasia is in the parts supplied by the left middle cerebral artery, particularly the lobe of the insula, or the island of Reil; and it is a curious fact that this part is found only in man and monkeys, being in the latter very slightly developed. While we must agree with most authors in the statement that the organ of language cannot be absolutely restricted to these parts, it is none the less certain that they are most frequently the seat of lesion in aphasia.

While it is demonstrated that the cerebral lesion in aphasia involves the left anterior lobe in the great majority of cases, there are several instances in which the right lobe alone is affected; and this has led physiologists and pathologists to deny the absolute location of the organ of language upon the left side. Even if we reject a certain number of cases of aphasia with the brain-lesion limited to the right side, in which we may suppose that the post-mortem examinations were incomplete, or the impairment of speech was due, perhaps, to simple paralysis of muscles, we must admit that, in a few instances, aphasia has followed injury or disease of the brain upon the right side. Aside from the anatomical arrangement of the arteries, which seem to furnish a greater amount of blood to the left hemisphere, it is evident that, as far as voluntary movements are concerned, the right hand, foot, eye, etc., are used in preference to the left; and that the motor functions of the left hemisphere are superior in activity to those of the right. It would be interesting, then, to note the physical peculiarities of persons affected with left hemiplegia and aphasia. Dr. Bateman quotes two cases of aphasia dependent upon lesion of the right side of the brain and consequent left hemiplegia, in which the persons were left-handed; and these, few as they are, are interesting, as showing that a person may use the right side of the brain in speech, as in the other motor functions. In this connection, it may not be uninteresting to note that, although most anatomists have failed to find any marked difference in the weight of the two cerebral hemispheres, Dr. Boyd has shown by an "examination of nearly two hundred cases at St. Marylebone, in which the hemispheres were weighed separately, that almost invariably the weight of the left exceeded that of the right by at least the eighth of an ounce." To conclude our citations of pathological facts bearing upon the location in the brain of the organ of speech, we may refer to an account, by Dr. Broadbent, of the brain of a deaf and dumb woman. In this case the brain was found to be of about the usual weight, but the left third frontal convolution was of "comparatively small size and simple character."

Taking into consideration all of the pathological facts bearing upon the subject, it seems certain that, in the great majority of persons, the organ or part presiding over the faculty of articulate language is situated at or near the third frontal convolution and the island of Reil in the left anterior lobe of the cerebrum, and mainly in the parts nourished by the middle cerebral artery. In some few instances, the organ seems to be located in the corresponding part upon the right side. It is possible that, originally, both sides preside over speech, and the superiority of the left lobe of the brain over the right and its more constant use by preference in right-handed persons may lead to a gradual abolition of the functions of the right side of the brain, in connection with speech, simply from disuse. This view, however, is hypothetical, but it is rendered probable by certain considerations, among the most important of which is the statement by Longet, that "one cerebral hemisphere in a healthy condition may suffice for the exercise of intelligence and the external senses." In support of this statement, Longet cites several cases of serious injury of one hemisphere without impairment of the intellect. In what is called the ataxic form of aphasia, the idea and memory of words remain, and there is simply loss of speech from inability to coördinate the muscles concerned in articulate language. Patients affected in this way cannot speak but can write with ease and correctness. In the amnesic form of the disease, the idea and memory of language are lost; patients cannot speak, and are affected with agraphia, or inability to write. In cases in which hemiplegia is marked, the aphasia is usually of the ataxic form; while, in cases in which there is no hemiplegia, the aphasia is generally amnesic.

The Cerebellum.

It is not necessary, in order to comprehend the functions of the cerebellum, as far as these are known, to enter into a full description of its anatomical characters. The points, in this connection, that are most interesting to us as physiologists are the following: the division of the substance of the cerebellum into gray and white matter; the connection between the cells and fibres; the connection of the fibres with the cerebrum, and with the prolongations of the columns of the spinal cord; and the passage of fibres between the two lateral lobes. These points, therefore, will be the only ones that will engage our attention.

As we have seen, in treating of the general arrangement of the encephalon, the cerebellum, situated beneath the posterior lobes of the cerebrum, weighs about 5·2 ounces av. in the male, and 4·7 ounces in the female. The proportionate weight to that of the cerebrum is as 1 to $8\frac{4}{7}$ in the male, and as 1 to $8\frac{1}{4}$ in the female. It is separated from the cerebrum by a strong process of the dura mater, called the tentorium. Like the cerebrum, the cerebellum presents an external layer of gray matter, the interior being formed of white, or fibrous nerve-tissue. The amount of the gray substance is very much increased by numerous fine convolutions and is farther extended by the penetration, from the surface, of arborescent processes of gray matter. Near the centre of each lateral lobe, embedded in the white substance, is an irregularly-dentated mass of cellular matter, called the corpus dentatum. The cerebellar convolutions are more numerous and the gray substance is deeper than in the cerebrum; and these convolutions are present in many of the inferior animals in which the surface of the cerebrum is smooth.

The cerebellum consists of two lateral hemispheres, more largely developed in man than in the inferior animals, and a median lobe. The hemispheres are subdivided into smaller lobes, which it is unnecessary to describe. Beneath the cerebellum, bounded in front and below by the medulla oblongata and pons, laterally by the superior peduncles, and superiorly by the cerebellum itself, is a lozenge-shaped cavity, called the fourth ventricle. The crura, or peduncles, will be described in connection with the direction of the fibres.

The structure of the gray substance of the convolutions presents certain peculiarities.

This portion is divided quite distinctly into an internal and an external layer. The internal layer presents an exceedingly delicate net-work of fine nerve-fibres, which pass to the cells of the external layer. In the plexus of anastomosing fibres, are found numerous bodies like free nuclei, called by Robin, myelocytes. The external layer is somewhat like the external layer of gray substance of the posterior lobes of the cerebrum

FIG. 227.—*Cerebellum and medulla oblongata.* (Hirschfeld.)

1, 1, corpus dentatum; 2, tuber annulare; 3, section of the middle peduncle; 4, 4, 4, 4, 4, 4, laminæ forming the arbor-vitæ; 5, 5, olivary body of the medulla oblongata; 6, anterior pyramid of the medulla oblongata; 7, upper extremity of the spinal cord.

and is more or less sharply divided into two or more secondary layers. The most external portion of this layer contains a few small nerve-cells and fine filaments of connective tissue; and the rest of the layer contains a great number of large cells, rounded or ovoid, with two or three, and sometimes, though rarely, four prolongations. The mode of connection between the nerve-cells and the fibres has already been described under the head of the general structure of the nervous system.

Course of the Fibres in the Cerebellum.—Most anatomical writers give a very simple description of the course of the nerve-fibres in the cerebellum. From the gray substance of the convolutions and their prolongations, the fibres converge to form finally the three crura, or peduncles on each side. The superior peduncles pass forward and upward to the crura cerebri and the optic thalami. These connect the cerebellum with the cerebrum. Beneath the tubercular quadrigemina, some of these fibres decussate with the corresponding fibres upon the opposite side; so that certain of the fibres of the superior peduncles pass to the corresponding side of the cerebrum, and others pass to the cerebral hemisphere of the opposite side.

The middle peduncles arise from the lateral hemispheres of the cerebellum, pass to the pons Varolii, where they decussate, connecting together the two sides of the cerebellum.

The inferior peduncles pass to the medulla oblongata and are continuous with the restiform bodies, which, in turn, are continuations chiefly of the posterior columns of the spinal cord.

From the above sketch, the physiological significance of the direction of the fibres, as it appears from the most reliable and generally-accepted anatomical investigations, is sufficiently evident. By the superior peduncles, the cerebellum is connected, as are all of the encephalic ganglia, with the cerebrum; by the middle peduncles, the two lateral halves of the cerebellum are intimately connected with each other; and, by the inferior peduncles, the cerebellum is connected with the posterior columns of the spinal cord. We shall see, when we come to study the functions of the cerebellum, that its connection with the posterior white columns of the cord is a point of great interest and importance.

General Properties of the Cerebellum.—There is now no difference of opinion among physiologists, with regard to the general properties of the cerebellum. Flourens, who made the first elaborate and satisfactory observations upon the cerebellum in living animals, noted, in all of his experiments, that lesion or irritation of the cerebellum alone produced neither pain nor convulsions; and the same results have followed the observations of all modern physiologists who have investigated this question practically. We have ourselves frequently exposed and mutilated the cerebellum in pigeons and have never observed any evidence of excitability or sensibility. From these facts, we must conclude that the cerebellum is inexcitable and insensible to direct stimulation, at least as far as has been shown by direct observations. It is not impossible, however, that future experiments may reverse this generally-received opinion; particularly in view of the recent observations of Fritsch and Hitzig, already cited, which show that certain parts of the cerebrum are excitable, and that the excitability of the encephalic centres rapidly disappears in living animals, as the result of pain and hæmorrhage. We should note, also, the experiments of Budge, who observed movements in the testicles and vasa deferentia, in males, and in the cornua of the uterus and in the Fallopian tubes, in females, following irritation of the cerebellum.

Functions of the Cerebellum.

There are still the widest differences of opinion among physiologists, with regard to the functions of the cerebellum, mainly for the reason that the experiments upon the lower animals, though in themselves sufficiently definite, are apparently contradicted by pathological observations upon the human subject. There should be no such discrepancy between well-conducted experiments and carefully-observed cases of disease or injury; for it is certain that the functions of the cerebellum present no essential differences in different animals, at least in man, the mammalia, and birds. It is necessary, therefore, for the physiologist, by carefully analyzing and correcting the results obtained by direct experimentation and by applying to the study of pathological observations the facts elicited by these experiments, to endeavor to harmonize the real or apparent contradictions; for, as we have often had occasion to remark, there are no exceptions to the laws to which the functions of similar classes of animals are subordinated; and observations and experiments, apparently discordant, will always be found, as our positive knowledge advances, to present differences in the conditions under which the phenomena have been observed. To apply this idea to the functions of the cerebellum, it may be safely assumed that it is impossible for this organ to preside directly and exclusively over muscular coördination in birds and the inferior mammals, and, in man, to possess different functions. With regard to the cerebrum, man possesses, not only a higher degree of development of certain intellectual faculties than the inferior animals, but is endowed with others, such as the power of articulate language. But, in man and in the higher orders of animals, the general properties and functions of the muscular system are essentially the same. To take one of the most generally-accepted views of the functions of the cerebellum, if this be the centre for muscular coördination in birds and mammals, it has the same office in man, although it may possess additional functions not found lower in the scale of animal life. Keeping in view, then, the desirability of bringing into accord the results of experiments and of pathological observations, we shall first study carefully the phenomena which follow injury or extirpation of the cerebellum in the lower animals.

Extirpation of the Cerebellum in the lower Animals.—In birds, and in certain mammals in which the operation has been successful, the more or less complete extirpation of the cerebellum is followed by well-marked phenomena, which present always the same character but are somewhat differently interpreted by various experimenters. Experiments of this kind were first made by Flourens; and the accuracy of his observations has never been successfully controverted, whatever may have been said of his physiological deductions. Indeed, there are few if any important points in the phenomena following partial or complete removal of the cerebellum that escaped the attention of this most accurate observer.

Laying aside, for the present, the deductions to be made from experiments upon animals, we may quote the following phenomena noted by Flourens and by all who have repeated his observations upon the cerebellum:

"I extirpated the cerebellum by successive layers in a pigeon. During the removal of the first layers, there only appeared slight feebleness and want of harmony in the movements.

"At the middle layers, there was manifested an almost universal agitation, although there was not added any sign of convulsion; the animal executed sudden and disordered movements; it heard and saw.

"On the removal of the last layers, the animal, the faculty of jumping, flying, walking, and maintaining the erect position being more and more disturbed by the preceding mutilations, lost this faculty entirely.

"Placed on the back, it was not able to recover itself. Far from resting calm and steady, as occurs in pigeons deprived of the cerebral lobes, it became vainly and continually agitated, but it never moved in a firm and definite manner.

"For example, it saw a blow with which it was threatened, wished to avoid it, made a thousand efforts to avoid it, but did not succeed. If it were placed on its back, it would not rest, exhausted itself in vain efforts to get up, and finished by remaining in that position in spite of itself.

"Finally, volition, sensation, perception, persisted; the possibility of making *general movements* persisted also; but the *coördination of the movements* in regular and definite acts of locomotion was lost."

The above are the phenomena observed after total extirpation of the cerebellum. Voluntary movement, sensation, general sensibility, and the special senses, seem to be intact; but there is always a loss of the power of equilibrium, and the movements executed are never regular, efficient, and coördinate. Flourens farther states that animals operated upon in this way retain their intellectual and perceptive faculties.

It is exceedingly important now to note the effects of partial removal of the cerebellum, as these bear directly upon cases of disease or injury of this organ in the human subject, in which its disorganization is very rarely complete. We may illustrate this, also, by citing two of Flourens's typical experiments:

"I. I removed by successive layers, all of the upper half of the cerebellum in a young cock.

"The animal immediately lost all stability, all regularity in its movements; and its tottering and *bizarre* mode of progression reminded one entirely of the gait in alcoholic intoxication.

"Four days after, the equilibrium was less disturbed, and the progression was more firm and assured.

"Fifteen days after, the equilibrium was completely restored.

"II. I removed, in a pigeon, about the half of the cerebellum; and I removed this organ completely in a fowl.

"At the end of a certain time, the pigeon had regained its equilibrium; the fowl did not regain it at all: the latter lived nevertheless for more than four months after the operation."

These important observations we have repeatedly confirmed, and we have in our possession the encephalon of a pigeon which recovered completely after removal of about two-thirds of the cerebellum, the animal first presenting marked deficiency in coördinating power.

Such are the phenomena observed in experiments upon the cerebellum in birds, and they have been extended by Flourens and others to certain mammals, as young cats, dogs, moles, mice, etc. Our own experiments, which have been very numerous during the last fifteen years, are simply repetitions of those of Flourens, and the results have been the same without exception.

The only difficulties in operating upon the cerebellum arise from hæmorrhage and the danger of injuring the medulla oblongata. The skull is exposed by slitting up the scalp, and the calvarium is removed in its posterior portion, penetrating just above the upper insertion of the cervical muscles. It is well to leave a strip of bone in the median line, thereby avoiding hæmorrhage from the great venous sinus, although this precaution is not essential. The cerebellum is thus exposed and may be removed in part or entirely, by a delicate scalpel or forceps, when the characteristic phenomena just described are observed. Animals operated upon in this way feel the sense of hunger and attempt to eat, but, when the movements are very irregular, they are unable to take food. We have frequently compared the phenomena presented after removal of the cerebellum with the movements of a pigeon intoxicated by forcing down the œsophagus a little bread impregnated with alcohol, and they present a striking similarity.

In view of the remarkable uniformity in the actual results obtained by different experimenters, it is hardly necessary to cite all of the observations made upon the lower animals. The phenomena observed by Flourens have been in the main confirmed by Fodéra, Bouillaud, Magendie, Wagner, Lussana, Dalton, Vulpian, Mitchell, Onimus, and many others. Certain of these authors differ from Flourens in their ideas concerning the functions of the cerebellum, while they admit the accuracy of his observations.

We shall eliminate from the present discussion the experiments made upon animals low in the scale, such as frogs and fishes (although, in some of these, the results are in accord with the observations just cited upon birds and mammals), and shall confine ourselves to an interpretation of the phenomena observed after extirpation of the cerebellum in animals in which the muscular and nervous arrangement is like that of the human subject. The results of this mutilation are as definite, distinct, and invariable, as in any experiments upon living animals, and, taken by themselves, they lead inevitably to but one conclusion.

When the greatest part or the whole of the cerebellum is removed from a bird or a mammal, the animal being, before the operation, in a perfectly normal condition and no other parts being injured, there are no phenomena constantly and invariably observed except certain modifications of the voluntary movements. The intelligence, general and special sensibility, the involuntary movements, and the simple faculty of voluntary motion, remain. The movements are always exceedingly irregular and incoördinate; the animal cannot maintain its equilibrium; and, on account of the impossibility of making regular movements, it cannot feed. This want of equilibrium and of the power of coördinating the muscles of the general voluntary system causes the animal to assume the most absurd and remarkable postures, which, to one accustomed to these experiments, are entirely characteristic. Call this want of equilibration, of coördination, of "muscular sense," an indication of vertigo, or what we will, the fact remains, that regular and coördinate muscular action in standing, walking, or flying, is impossible, although voluntary power remains. It is well known that many muscular acts are more or less automatic, as in standing, and, to a certain extent, in walking. These acts, as well as nearly all voluntary movements, require a certain coördination of the muscles, and this, and this alone, is abolished by extirpation of the cerebellum. It is true that destruction of the semicircular canals of the internal ear produces analogous disorders of movement, but this is the only mutilation, except division of the anterior white columns of the spinal cord, which produces any thing resembling the results of cerebellar injury. Certain important coördinate muscular movements are well known to be dependent upon distinct nerve-centres. The acts of respiration are presided over exclusively by the medulla oblongata. Deglutition probably has its distinct nerve-centre, as well as the movements of the eyes. The centre regulating the coördinate movements in speech is situated in the anterior cerebral lobes. None of these peculiar movements are affected by extirpation of the cerebellum.

If there be a distinct nerve-centre which presides over the coördination of the general voluntary movements, experiments upon the higher classes of animals show that this centre is situated in the cerebellum. It may be either in the entire cerebellum or in a certain portion of this organ, but, if it be confined to a restricted part, this has not yet been determined. If the cerebellum preside over coördination, as a physiological necessity, the centre must be connected by nerves with the general muscular system. If this connection exist, a complete interruption of the avenue of communication between the cerebellum and the muscles, we should naturally expect, would be followed by loss of coördinating power. From the anatomical connections of the cerebellum, it appears that the only communication between this organ and the general system is through the posterior white columns of the spinal cord. We have seen that these columns are not for the transmission of the general sensory impressions, and there is no satisfactory evidence that they convey to the encephalon the so-called muscular sense. As regards general sensibility and voluntary motion, we cannot ascribe any function to the posterior white columns, except that, when they are divided at several points, we invariably have want of coördination of the general muscular system. When the posterior white columns are disorganized in the human subject, we have loss or impairment of coördinating power, even though the general sensibility be not affected, as in the disease called locomotor ataxia.

Confining ourselves still to the interpretation of experiments upon living animals, and leaving for subsequent consideration the phenomena observed in cases of disease or injury of the cerebellum in the human subject, we are led to the following conclusions:

There is a necessity for coördination of the movements of the general voluntary system of muscles, by means of a nerve-centre or centres.

Whatever other functions the cerebellum may have, it acts as the centre presiding over equilibration and general muscular coördination.

The cerebellum has its nervous connections with the general muscular system through the posterior white columns of the spinal cord, a fact which is capable both of anatomical and physiological demonstration.

If the cerebellum be extirpated, there is loss of coördinating power; and, if the posterior white columns of the cord be completely divided, destroying the communication between the cerebellum and the general system, there is also loss of coördinating power.

When a small portion only of the cerebellum is removed, there is slight disturbance of coördination, and the disordered movements are marked in proportion to the extent of injury to the cerebellum.

After extirpation of even one-half or two-thirds of the cerebellum, the disturbances in coördination immediately following the operation may disappear, and the animal may entirely recover, without any regeneration of the extirpated nerve-substance. This important fact enables us to understand how, in certain cases of disease of the cerebellum in the human subject, when the disorganization of the nerve-tissue is slow and gradual, there may never be any disorder in the movements.

We present the above conclusions, as in our own mind positive and definite. It is proper to state, however, that the definition of the function of the cerebellum is one of the points stated by many physiological authors as doubtful and unsettled; and this is so, mainly because some writers have been unable to harmonize the experimental facts above detailed, with cases of disease or injury of the cerebellum in the human subject. We conceive that this has frequently been due to an imperfect study of the pathological facts, which we now propose to discuss.

Pathological Facts bearing upon the Functions of the Cerebellum.—Nearly all writers upon the physiology of the nervous system, while they agree that extirpation of the cerebellum in the lower animals produces irregularity of movements, are arrested, as it were, in their deductions, by the following quotation from Andral, in his report of ninety-three cases of disease of the cerebellum:

"A more remarkable alteration of movement is noted in the observation of M. Lallemand. The patient staggered on his legs, and often came near falling forward. In this case, the only one which tends to confirm the opinion of physiologists who regard the cerebellum as the organ of the coördination of movements, the cerebellum was entirely transformed into a sac filled with pus."

The bare statement, such as is generally made, that Andral collected ninety-three cases of disease of the cerebellum, only one of which tends to show that this is the organ of muscular coördination, is sufficient to arrest any physiologist in the conclusions that would naturally be drawn from experimental facts; and many writers have expressed themselves as uncertain upon the question of the function of the cerebellum. Before we go any farther, we wish to settle, once for all, the physiological bearing of these cases; and, with this end in view, have carefully studied, analyzed, and tabulated them. Out of the ninety-three cases, fifteen were observed by Andral, and seventy-eight are quoted from various authors. An analysis of these cases, with reference to conditions likely to complicate the effects of the cerebellar disease, etc., is given in the following table:

Analysis of Andral's Ninety-three Cases of Disease of the Cerebellum.

(Six Cases, observed by Andral.[1]*)*

Hemiplegia; death in fifty hours	1 case.
Hemiplegia; sudden death	1 "
Hemiplegia; death in two days	1 "
Hemiplegia; associated with cerebral hæmorrhage	3 "

(Seventy-eight Cases, quoted from various Authors.)

Hæmorrhage into the cerebellum; quoted from Serres	6 * cases.
" " " quoted from Dance	1 † case.
" " " quoted from Bayle	1 ‡ "
" " " quoted from Guiot	1 § "
" " " (Serres); hemiplegia	2 cases.
" " " (Cazes); coma	1 case.
" " " (Morgagni); found dead	1 "
" " " (Sédillot); died in fifteen minutes	1 "
" " " (Cafford); died suddenly	1 "
Hæmorrhage (Michelet); apoplexy two years before death; found an old clot in the right lobe of the cerebellum	1 "
Hæmorrhage (quoted from various authors); hæmorrhage into the cerebrum as well as the cerebellum	9 cases.
Atrophy of the left cerebral and the right cerebellar hemisphere	2 "
Cases of disease, with paralysis; quoted from various authors	9 "
Cases of abscess, with paralysis; quoted from various authors	3 "
Cyst (Récamier); convulsions	1 case.
Abscess (Laugier); convulsions	1 "
Abscess, involving the entire cerebellum (Lallemand); want of coördination[2]	1 "
Cases, quoted from various authors, in which no disturbance was noted in the movements; the disease was confined to one lateral lobe of the cerebellum	5 cases.

[1] In these six cases, there was hæmorrhage into the cerebellum.

[2] This is the single case, noted by Andral, out of the ninety-three, the only one showing want of coördination.

Cases of tumor, quoted from various authors, in which there was paralysis . .	15	cases.
Cases of tumor, associated with disease of the cerebrum	7	"
Cases of tumor, associated with convulsions; the descriptions are very indefinite .	9	"

(*Nine Cases, observed by Andral.*)

Softening; hemiplegia and convulsions	1	case.
Softening; hemiplegia and subsequent hæmorrhage	1	"
Softening; hemiplegia and hæmorrhage	1	"
Softening; agitation, like convulsions, of the members	1	"
Cyst; paralysis and convulsions	1	"
Tubercle; hemiplegia	1	"
Five small tubercles in one hemisphere of the cerebellum; movements normal . .	1	"
Tuberculous mass, the size of a hazel-nut, on one side of the cerebellum; movements normal	1	"
Cyst, the size of a hazel-nut, on one side of the cerebellum; movements normal .	1—9	cases.
Add cases of hæmorrhage, previously cited, observed by Andral, ...	6	"
Add cases quoted from various authors	78	"
Total cases collected by Andral	93	cases.

In six cases, quoted from Serres, marked *, "there were observed all the signs of violent apoplexy; nothing in particular is said with regard to disorders of movement." In the case quoted from Dance, marked †, the patient was struck with apoplexy. In the case quoted from Bayle, marked ‡, the patient suddenly lost consciousness, had convulsive movements on the third day, and died in coma, on the fifth day. In the case quoted from Guiot, marked §, there was "no lesion except effusion of blood in the median lobe of the cerebellum. The individual who was the subject of this observation had had an attack of apoplexy. Before his attack, he had for some time a tottering gait (*démarche chancelante*), and, after the attack, remained hemiplegic on the right side."

Let us now carefully review these ninety-three cases of Andral, which have been held *in terrorem* over those who have ventured to argue, from experiments upon animals, that the cerebellum is the coördinator of the muscular movements, and see how many may properly be thrown out of the question!

We can discard the first six cases, observed by Andral, in which there was hemiplegia, speedy death, and in three of which there was cerebral hæmorrhage; for we could hardly observe want of coördination in hemiplegics or in cases complicated with cerebral disease. We can discard the six cases, quoted from Serres, in which there was violent apoplexy, as well as the case quoted from Dance, with apoplexy, and the case quoted from Bayle, with coma and convulsions. It is evident that these cases are useless in noting the presence or absence of coördinating power. We can discard two cases, (Serres) with hemiplegia; one, (Cazes) with coma; one, (Morgagni) found dead; one, (Sédillot) died in fifteen minutes; one, (Cafford) died suddenly; and one, (Michelet) apoplexy two years before death, and an old clot in the right lobe of the cerebellum. This last case is in accord with experiments on animals; for we have seen that the coördinating power may be restored after loss of one-half of the cerebellum. We can discard nine cases quoted from various authors, in which there was cerebral as well as cerebellar hæmorrhage; two cases of paralysis, with atrophy of one hemisphere of the cerebrum and one hemisphere of the cerebellum; nine indefinitely-described cases, with paralysis; three cases of abscess, with paralysis; one case of cyst and one of abscess, with paralysis; fifteen cases of tumor, with paralysis; seven cases, associated with disease of the cerebrum and paralysis; and nine very indefinitely described cases, associated with convulsions. Of the remaining cases observed by Andral, we can discard one, with hemiplegia and convulsions; one, with hemiplegia and subsequent hæmorrhage; one, with hemiplegia; one case of cyst, with paralysis and convulsions; and one, of tubercle, with hemiplegia. We can also discard one case of five small tubercles in one hemisphere of the cerebellum; one, of a tuberculous mass, the size of a hazel-nut, upon one side; and one, of a cyst, the size of a hazel-nut, upon one side. These last cases do not present sufficient destruction of the cerebellar substance to lead us to expect any disorder in the movements.

Thus far we have discarded eighty-five cases, leaving eight to be analyzed. Of these eight cases, in five, it is simply stated that the movements were unaffected, and that "one of the lateral lobes of the cerebellum was the seat of abscess." In view of this bare statement, and of the fact that, in animals, recovery of coördinating power takes place when half of the cerebellum has been removed, we may throw out these cases as incomplete. It must be remembered that the abscesses were probably of slow development; and, if they did not destroy a sufficiently large portion of the cerebellum to influence the coördinating power permanently, it is not probable that the functions of this organ would be at all affected, as there would be no shock, such as occurs in the sudden removal of substance by an operation.

We are thus reduced to three cases; and, in all of these, the movements were more or less affected. These cases we shall now study as closely as is possible from the details given.

Case I.—The first case is quoted from Guiot. There was no lesion, except an effusion of blood in the median lobe of the cerebellum, and there was probably no pressure upon the peduncles. "The individual who was the subject of this observation had had an attack of apoplexy. Before the attack, he had for some time a staggering gait (*une démarche chancelante*), and, after the attack, he had remained hemiplegic on the left side." From these meagre details, it seems probable that there was a certain amount of difficulty of coördination, although the description is not as definite as could be desired.

Case II.—The second case was observed by Andral. A groom, not quite forty years of age, was brought into the *Maison royale de santé*, having suffered from severe headache, vertigo, etc., for fifteen days, which finally became fixed at the occiput. During the first three days in the hospital, "he was in a continual state of agitation; the movements of the members, on the right as well as the left side, were sometimes so *brusques* and disordered that they resembled convulsive movements." Soon the respiration became disturbed, and he died in asphyxia. "Upon post-mortem examination, there was found general injection of the meninges; nothing particular in the cerebral hemispheres; a moderate quantity of serum in the ventricles; reddish softening of the left hemisphere of the cerebellum in its posterior and inferior half; no other lesion."

The only marked symptom relating to the movements in this case was a certain amount of irregularity and convulsive action of the muscles, while the patient was in bed. The case is not strong in its bearings, either for or against the coördination-theory; for there must have been a great amount of irritation of the encephalic centres, and it would certainly be difficult to note disturbance of equilibration or of coördination in a patient confined to the bed.

The third case is quoted by Andral from Lallemand, and is taken by Lallemand from Delamare.

Case III.—"M. Guérin, vicar at Gézeville, forty-six years of age, of a good temperament, strong, and corpulent, with a good appetite, complained of a dull pain, which finally became acute, under the frontal bone. For a year he experienced attacks of vertigo and vomiting, without fever. He staggered on his legs, and was often near falling forward. The treatment employed was antiphlogistic and derivative."

On post-mortem examination, the cerebrum was found entirely healthy, but the envelop of the cerebellum was collapsed, folded, and only contained about the half of an egg-shell full of a brown and fetid, lymphatico-purulent liquid.

This case, as far as the description goes, shows marked difficulty in equilibration or coördination.

If the reader have carefully studied the foregoing analysis of Andral's cases, he will see that eighty-five may be thrown out altogether, leaving but eight; and, of these eight cases, five are so imperfectly described, and the disorganization of the cerebellum is so restricted, that they may also be disregarded. The ninety-three cases are thus reduced to three. Of these three cases, in two, it is uncertain whether or not there were deficiency of coördinating power; and in one, the difficulty in equilibration or coördination was distinctly noted. This, we conceive, disposes of the much-quoted ninety-three cases of Andral; and they are certainly not opposed to the view that the cerebellum is the organ of equilibration or muscular coördination.

In addition to the cases collected by Andral, there are numerous other instances on record of disease confined to the cerebellum, of which the following are examples:

Case IV.—In 1826, Petiet reported a case of disease, in which the cerebellum was entirely destroyed, its tissue being broken down into a sort of whitish *bouillie.* The cerebrum was healthy. The observation was made in 1796. The patient, before death, was observed to present a remarkable tendency to walk backward. He rose from his seat with difficulty, and, once erect, the first movements of the feet were lateral, and he finally walked by moving the feet from before backward. His locomotion consisted simply in passing from his own to an adjoining bed in the ward, a distance of about six feet.

Case V.—One of the most remarkable cases, and the one most frequently quoted by physiological writers, was reported by Combette, in 1831. This patient, Alexandrine Labrosse, in her seventh year, was seen by M. Miquel. Since the age of five years only had she been able to sustain herself on her feet. M. Miquel was struck with her slight development and the feebleness of the extremities. At the age of nine and a half years, she was admitted into the *Orphelins.* "When spoken to, she answered with difficulty and hesitation. Her legs, although very feeble, enabled her still to walk, but she often fell." She was first seen by M. Combette, in January, 1831. She had then kept the bed for three months; was constantly lying on the back, and could scarcely move the legs; she used her hands with ease. She died of some intestinal disorder, March 25, 1831. On post-mortem examination, "in place of the cerebellum there was a cellular membrane, gelatiniform, semicircular, from eighteen to twenty lines in its transverse diameter." There was no trace of the pons Varolii. Combette states that Alexandrine Labrosse was able to walk for several years, always, it is true, in an uncertain manner; later, her legs became more and more feeble, and finally she ceased to be able to sustain her weight. She had the habit of masturbation. Combette farther states that this observation is not in accord "with the experiments of Flourens, which tend to show that the cerebellum is the regulator of movements." The encephalon was also examined by Guillot, who noted absence of the cerebellum and of the pons.

This case is somewhat imperfect, as it was not seen by Combette until the patient had kept the bed for three months. By some writers, it is quoted in favor of, and by some, in opposition to the view that the cerebellum coördinates the muscular movements. It was not a case of simple disease of the cerebellum, as the pons and the posterior peduncles were also absent. It was noted, before the case was seen by Combette, that the patient walked in an uncertain manner and often fell.

Several cases of injury of the cerebellum are reported by Larrey.

Case VI.—One case is described, in which the patient was struck by a ball from a blunderbuss, which grazed the occipital protuberances. There was no disturbance of movement. The patient died on the thirty-ninth day, in opisthotonos. On post-mortem examination, "the occipital bone had sustained a considerable loss of substance; the slit into the dura mater, to which we have alluded, corresponded to the centre of the right lobe of the cerebellum, which was sunk downward and was of a yellowish color, but free from suppuration or effusion. The medulla oblongata and spinal marrow bore a dull, white aspect, were of greater consistence than is natural, and had lost about a quarter of their size; the nerves arising from them appeared to us also to be in a state of atrophy near their origin."

CASE VII.—Another patient was struck by a piece of wood on the right side of the head. He was found dead a little more than three months after the injury. "The right hemisphere of the cerebellum was entirely disorganized by an abscess which pervaded its whole substance." No disturbances of movement were noted.

CASE VIII.—Another patient had erysipelas following a fall on the side of the head, and abscess. He lived for three or four months. Five or six weeks after the injury, he had severe pains in the occiput, and, "when standing, he could with difficulty only preserve his equilibrium." On post-mortem examination, the deep-seated vessels of the cerebrum were found injected. "We found, in the left lobe of the cerebellum, about three table-spoonfuls of pus of a whitish and gelatinous aspect, which had encroached upon, or rather displaced entirely, the hemisphere of the cerebellum; this purulent substance was enveloped within the pia mater, which had acquired a somewhat firmer consistence, and, as in the subject of the preceding case, assumed a pearly color. The other half of the cerebellum was shrivelled, and the medullary substance forming the arbor-vitæ was of a grayish color and very dense."

The first of these cases was found by Larrey to be associated with extinction of sexual appetite and atrophy of the organs of generation. In the first two cases, judging from the results of experiments on animals, there was not enough injury of the cerebellum to necessarily influence the power of coördination. In the last case, there was difficulty in equilibration, but also some paralysis.

A number of cases, which it is unnecessary to detail fully, are cited by Wagner, in the *Journal de la physiologie*, 1861, in which tottering gait and want of equilibration or of muscular coördination were noted, in connection with greater or less disorganization of the cerebellum. In the same journal, is a brief note of a case, reported by Laborde, in which there was a large cyst in the cerebellum, with incomplete paraplegia and "want of coördination of the movements of progression."

CASE IX.—A most remarkable and carefully-observed case of atrophy of the cerebellum was reported by Dr. Fiedler, in 1861. The subject of this observation, a man, aged about fifty years, had remarkable peculiarities in his movements for thirty years. After the age of twenty years, it is stated that "he could no longer walk with as much certainty as before; the gait was staggering (*taumelnd*). . . . Not only in the house, but also in the street, the patient often fell, so that he was very frequently taken for a drunkard, and was either carried home or taken to the police-station. It is said that he never had drunk spirituous liquors.

"Sometimes the patient walked backward, but only a few steps. He never had any turning movements; the gait was always tottering (*wacklig*) and slow." He never fell forward, but always on the back. On post-mortem examination, the cerebrum was found healthy, "but the cerebellum was atrophied, especially at its posterior and inferior portion, and was reduced in size at least one-half." This case presented the phenomena of defective coördination to a marked degree. Nothing is said of vertigo.

Among the most striking of the cases of disease of the cerebellum, are two observed by Vulpian.

CASE X.—The first was a woman, forty-nine years of age, in the hospital of *la Salpêtrière*. "All of the movements were preserved, but locomotion was most irregular and difficult; she could only walk in the most *bizarre* manner, resting on a chair which she placed before her at every step, and, in spite of her efforts at equilibration, she often fell." This patient, however, retained great muscular power. On post-mortem examination, "the cortical gray substance of the cerebellum was found entirely atrophied: all the nerve-cells of this layer had disappeared." There was considerable reduction in the size of the cerebellum. The corpora dentata were perfectly preserved, "showing that these parts, at all events, have but a slight office in coördination."

CASE XI.—The second case presented an old softening, about the size of a hazel-nut, destroying a corresponding amount of the cerebellar substance of one of the hemispheres. The corpus dentatum was completely destroyed. This woman "walked well, but it appears nevertheless that she vacillated very slightly in her gait, without, however, a tendency to fall."

We have thus cited quite a number of cases of disease confined to the cerebellum, in which there was marked disturbance in the muscular movements; but there are others, in which the movements were unaffected. As an example of the latter, we may refer to a case quite fully reported by Bouvier:

Case XII.—"A man, fifteen years of age, had been subject, for a length of time, to a discharge from the ear, with deafness and frequent headache. He was suddenly seized with more severe headache on the left side of the head, vomiting, and disorder of mind. His symptoms were, indeed, so characteristic, that a physician who was consulted pronounced him to be laboring under abscess in the head, and that death was almost certain.

"He entered the *Hôtel Dieu* on the 15th of September, three weeks after the last exacerbation, when he complained of fixed pain in the head, which frequently caused him to cry out; sensibility, in other respects, obtuse; slow answers; somnolency; face pale; features sunken; look, sad and anxious; a copious, purulent discharge from the left ear; deafness of the same side; pulse slightly slower; vomiting; constipation; the movements of the limbs were preserved, an incomplete paralysis of the upper eyelid being alone observed.

"These symptoms continued for the following days without any marked aggravation; and it seemed probable that the patient's life might still be prolonged for some time, when, on the 23d of September, after vomiting, accompanied by great agitation and violent outcry, he suddenly fell into a state of complete collapse. Respiration became embarrassed, and he died eight days after his entrance into the hospital, with symptoms of asphyxia.

"On examining the body, there was found, as had been foretold during life, a caries of the petrous portion of the temporal bone, and an abscess in the interior of the cranium. But what was remarkable, the abscess occupied the left hemisphere of the cerebellum, although nothing led to the suspicion that there was any lesion of that organ. There was an extensive cavity, which invaded the two outer thirds of the left lobe of the cerebellum, and which contained several table-spoonfuls of pus, somewhat similar to that of an abscess. The substance forming its parietes were softened and of a livid tint. The meatus auditorius was filled with reddish vegetations.

"The caries occupied the base of the pars petrosa only—the labyrinth and auditory nerve were untouched. There was no perceptible communication between the internal abscess and the abscess of the caries. The disease of the bone, however, extended to the dura mater, in two very circumscribed points, at the upper and hind part of the pars petrosa. The dura mater, opposite these points, was deeply colored; and its coloration extended to its inner surface, where it was in contact with the cerebellum.

"The cerebral ventricles were, moreover, distended by a limpid fluid; and the pia mater exhibited a decided injection under the anterior part of the cerebral lobes, chiefly on the left side.

"'Two circumstances,' says M. Bouvier, 'give interest to this case. The first is the almost entire separation, by means of the dura mater—which was scarcely affected—between two lesions, one of which must have been the effect of the other; so that it is difficult to explain, merely by continuity of tissue, the transmission of the affection from the ear to the cerebellum.

"'The second is the absence of all the symptoms which have been of late regarded as an effect of lesions of the cerebellum—such as augmentation of the general sensibility, loss of equilibrium, and excitation of the genital organs. Could this peculiarity be owing to the slowness of the affection, or to its not having extended sufficiently far from the side of the medulla oblongata?'"

The interpretation of certain of the cases which we have cited depends apparently upon the ideas concerning the functions of the cerebellum with which they are regarded. We should certainly consider those cases in which disordered movements have been noted, as very strong evidence, taken in connection with the results of experiments upon living animals, that the cerebellum regulates equilibration and muscular coördination. Some physiologists regard them as in accordance with the view that injury of the cerebellum does not affect coördination, but simply produces vertigo. It remains for the reader to judge whether or not the phenomena observed in these cases indicate want of coördinating power. In the case reported by Bouvier, the lesion of the cerebellum was not sufficient to necessarily disturb coördination.

We now come to the main question, whether or not, in view of the results of experiments upon animals and the phenomena observed in cases of disease or injury of the cerebellum, this nerve-centre presides over coördination of action of the muscles, which is certainly necessary to equilibration, except the muscles of the face and those concerned in speech. This question, it seems to us, can be definitely answered.

Every carefully-observed case that we have been able to find, in which there was uncomplicated disease or injury of the cerebellum, provided the disease or injury involved more than half of the organ, presented great disorder in the general movements, particularly those of progression. We have collected the more or less complete reports of twelve cases. In Case II., there was softening of one-half of one hemisphere, with remarkable convulsive movements. In Case V., the one so often quoted from Combette, the gait was uncertain, with frequent falling; there was incomplete paralysis; but, in addition to the absence of the cerebellum, there was no pons Varolii. In Case VI., there was no disturbance of movement, and there was partial degeneration of one lateral lobe of the cerebellum. In Case VII., there was no disturbance of movement, and disorganization of one lateral lobe of the cerebellum. In Case XI., there was slight loss of substance in one lateral lobe of the cerebellum, and slight "vacillation" in the movements. In Case XII., there was an abscess involving two-thirds of one lateral lobe, and the movements of the limbs were preserved. In Cases I., III., IV., VIII., IX., X., six out of twelve, there was difficulty in muscular coördination, which was invariably in direct ratio to the amount of cerebellar substance involved in the disease or injury. We do not make the reservation, that more than half of the cerebellum must be destroyed in order necessarily to produce difficulty in muscular coördination, upon purely theoretical grounds, but we regard this point as positively demonstrated by experiments upon animals. These experiments show that one-half of the organ is capable of performing the function of the whole. We have an analogy to this in the action of the kidneys, one of which is sufficient for the elimination of the effete constituents of the urine, after the other has been removed.

Notwithstanding the contrary views of many physiological writers, we are firmly convinced, from experiments and a careful study of pathological facts, that there is no one point in the physiology of the nerve-centres more definitely settled than that the cerebellum presides over equilibration and the coördination of the muscular movements, particularly those of progression. In this statement, we make exceptions in favor of the movements of respiration, deglutition, of the face, and of those concerned in speech, as well as the involuntary movements generally. As another example of a nerve-centre presiding over muscular coördination, we have the instance of the portion of the left anterior lobe of the cerebrum which coördinates the action of the muscles concerned in speech.

The theory that the disordered movements which follow injury of the cerebellum are due simply to vertigo is not tenable; and in only one of the cases cited is vertigo mentioned. There is a disease, involving the semicircular canals and other parts of the internal ear, called Ménière's disease, in which there is marked want of equilibration and muscular coördination, attended with, and probably dependent upon vertigo. The vertigo is always very distinct and is mentioned in all of these cases; and, although it is less in the recumbent posture, it is never entirely absent. A careful study of these cases, comparing them with the cases of deficient coördination from disease of the cerebellum, cannot fail to show a great difference between the phenomena following cerebellar disease and the muscular phenomena due to well-marked and persistent vertigo.

Connection of the Cerebellum with the Generative Function.—The fact that the cerebellum is the centre for equilibration and the coördination of certain muscular movements does not necessarily imply that it has no other functions. The idea of Gall, that "the cerebellum is the organ of the instinct of generation," is sufficiently familiar; and there are numerous facts in pathology which show a certain relation between this nerve-centre and the organs of generation, although the idea that it presides over the generative function is not sustained by the results of experiments upon animals or by facts in comparative anatomy.

In experiments upon animals in which the cerebellum has been removed, there is nothing pointing directly to this part as the organ of the generative instinct. Flourens removed a great part of the cerebellum in a cock. The animal survived for eight months. It was put several times with hens and always attempted to mount them, but without success, from want of equilibrium. In this animal, the testicles were enormous. This observation has been repeatedly confirmed, and there are no instances in which the cerebellum has been removed with apparent destruction of sexual instinct. In a comparison of the relative weights of the cerebellum in stallions, mares, and geldings, Leuret found that, far from being atrophied, the cerebellum in geldings was even larger than in either stallions or mares.

In the numerous cases of disease or injury of the cerebellum, to which we have referred, there are some, in which irritation of this part has been followed by persistent erection and manifest exaggeration of the sexual appetite, and others, in which its extensive degeneration or destruction has apparently produced atrophy of the generative organs and total loss of sexual desire. There are also certain cases of this kind which we have not yet cited. Serres gives the history of several cases, in which irritation of the cerebellum was followed by satyriasis or nymphomania, but, in other cases, there were no symptoms referable to the generative organs. In the case reported by Combette, the patient had the habit of masturbation. Dr. Fisher, of Boston, reported (1838) two cases of diseased or atrophied cerebellum, with absence of sexual desire, and one case of irritation, with satyriasis. Similar instances are given by other writers, which it is unnecessary to detail. We have already cited the observations of Budge, in which mechanical irritation of the cerebellum was followed by movements of the uterus, testicles, etc.

Although there are many facts in pathology which are opposed to the view that the cerebellum presides over the generative function, there are numerous cases which go to show a certain connection between this portion of the central nervous system and the organs of generation in the human subject. But this is all that we can say upon this important point; certain it is that the facts are not sufficiently numerous, definite, and invariable, to sustain the doctrine that the cerebellum is the seat of the sexual instinct.

Development of the Cerebellum in the Lower Animals.—The study of the comparative anatomy of the cerebellum has little physiological interest, except in so far as it bears upon our knowledge of its functions. From this point of view, there is little to be said concerning its development in the animal scale. We can hardly establish a definite relation between this particular part of the encephalon and the complicated character of the muscular movements; for, as we pass from the lower to the higher orders of animals, we have other parts of the brain, as well as the cerebellum, developed in proportion to the increased complexity of the muscular system. Nor can we connect the comparative anatomy of the cerebellum with the ideas of the functions of this organ in connection with generation. The amphioxus lanciolatus has no cerebellum, and this organ, therefore, is not indispensable to generation. In some animals remarkable for salacity, the cerebellum is not unusually large; and facts of this kind might be multiplied *ad infinitum*.

We have thus discussed only those views with regard to the functions of the cerebellum which are supported by experimental or pathological facts, and have not touched upon the vague and unsupported ideas advanced by various writers before the publication of the remarkable observations of Flourens. There is no proof that the cerebellum is the organ presiding over memory, the involuntary movements, general sensibility, or the general voluntary movements. The only view that has any positive experimental or pathological basis is that it presides over equilibration and the coördination of certain muscular movements, and is, perhaps, in some way connected with the generative function.

Ganglia at the Base of the Encephalon.

At the base of the encephalon, are found several collections of gray matter, or ganglia, some of which have functions distinct from those already described in connection with the cerebrum and cerebellum; but most of them are so difficult of access in living animals, that we possess very little definite information, even with regard to their general properties. We have, however, a tolerably complete knowledge of the functions of the medulla oblongata and the tubercula quadrigemina, and have some idea of the physiology of the tuber annulare; but the functions of the corpora striata, optic thalami, ventricles, pineal gland, peduncles, etc., are little understood, and the speculations of the older writers, with the indefinite experiments of modern physiologists, upon these parts, will be passed over very briefly.

Corpora Striata.

These bodies are somewhat pear-shaped, and are situated at the base of the brain, partly without the cerebral hemispheres and partly embedded in their white substance.

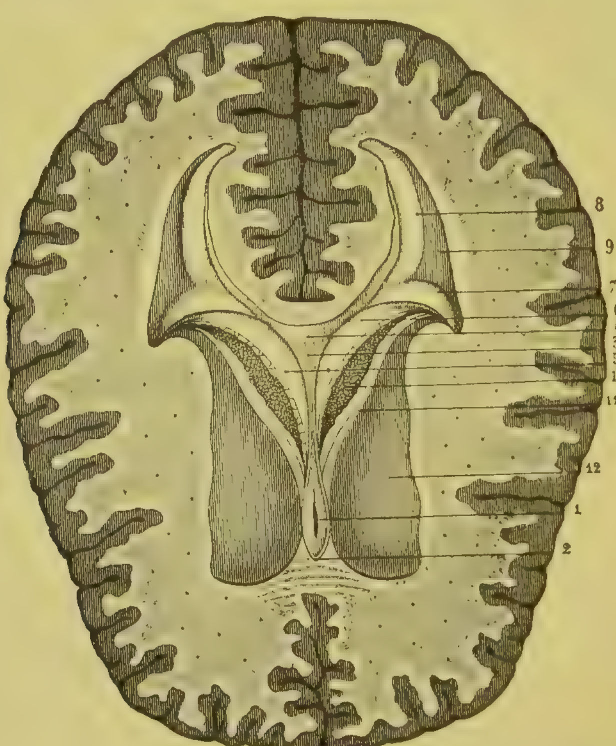


FIG. 228.—*Corpora striata.* (Sappey.)
1, fifth ventricle; 2, the two laminæ of the septum lucidum meeting in front of the fifth ventricle; 3, hippocampus minor; 4, posterior portion of the corpus callosum; 5, middle portion of the fornix; 6, posterior pillar of the fornix; 7, hippocampus major; 8, eminentia collateralis; 9, lateral portions of the fornix; 10, choroid plexus; 11, tænia semicircularis; 12, *corpus striatum.*

Their rounded base is directed forward, and the narrower end, backward and outward. Their external surface is gray, and they present, on section, alternate striæ of white and gray matter, which appearance has given them the name of corpora striata. Between the narrow extremities of these bodies, are situated the optic thalami.

There is very little to be said with regard to the functions of the corpora striata. Burdon-Sanderson has lately shown that, when the corpus striatum on one side, exposed by carefully removing a small portion of the anterior lobe of the cerebrum, is stimulated with a weak induced current of galvanism, movements of the muscles occur upon the opposite side of the body. If the deepest parts be stimulated, "the animal opens its mouth, puts out its tongue, and draws it in again alternately." When the corpora striata are removed, disturbing the hemispheres as little as possible, there appears to be no paralysis, either of motion or sensation.

We have obtained a little more information regarding the functions of the corpora striata, from cases of cerebral hæmorrhage in the human subject, than from experimental investigations. In apoplexy, when the corpus striatum on one side is alone involved, there is paralysis of motion of the opposite lateral half of the body, the general sensibility usually being unaffected. Facts of this kind show that the action of the corpora striata is crossed; and they farther illustrate their connection with the motor tract from the hemispheres.

There is no reason to suppose that the corpora striata are the centres of olfaction, as was at one time thought, for they are sometimes absent in animals possessing very large olfactory nerves, and they are very largely developed in the cetacea, in which the olfactory apparatus is rudimentary.

Optic Thalami.

From their name, we should infer that the optic thalami have some important function in connection with vision; but they serve merely as beds for the optic commissures and give to the nerves but very few fibres. They are oblong bodies, situated between the posterior extremities of the corpora striata, and resting upon the crura cerebri on the two sides. They are white externally, and, in their interior, present a mixture of white and gray matter. Longet has destroyed them upon the two sides, carefully avoiding injury of the optic tracts, and he noted no interference with vision or with the movements of the iris.

The optic thalami seem, from experiments upon animals, to have a peculiar crossed action upon the muscular system. While their mechanical irritation produces neither pain nor convulsive movements, showing that they are probably insensible and inexcitable, the extirpation of one optic thalamus is followed by enfeeblement of the muscles of the opposite lateral half of the body, without actual paralysis. When both have been removed, there is general debility of the muscular system. It is unnecessary to refer to other experiments upon these parts, which have been very indefinite in their results, or to allude to the "circular" movements produced by lesion upon one side, involving also the crus cerebri; for, beyond the statement just made, the function of the optic thalami is unknown.

We derive but little information concerning the optic thalami from cases of cerebral hæmorrhage in the human subject; for it is not common to have disease involving these parts and not affecting other centres. In some cases of lesion limited to the optic thalamus on one side, there is paralysis of sensation of the opposite lateral half of the body, without actual paralysis of motion, although the movements are generally feeble. When the brain-lesion involves both the corpus striatum and the optic thalamus on one side, which is more common, there is paralysis of motion, with loss or disorder of sensibility, on the opposite side of the body. These facts illustrate, to a certain extent, the anatomical connection of the optic thalami with the sensory tracts, although, in experiments upon animals, destruction of these parts does not necessarily affect the general sensibility.

Tubercula Quadrigemina.

These little bodies, sometimes called the optic lobes, are rounded eminences, two upon either side, situated just below the third ventricle. The anterior, called the nates, are the larger. These are oblong and of a grayish color externally. The posterior, called the testes, are situated just behind the anterior. They are rounded and are rather lighter in color than the anterior. Both contain gray nervous matter in their interior. They are the main points of origin of the optic nerves and are connected by commissural fibres with the optic thalami. In birds, the tubercles are two in number, instead of four, and are called tubercular bigemina.

It is probable that the tubercula quadrigemina are inexcitable and insensible. When pain and convulsive movements have apparently followed their mechanical irritation in living animals, these phenomena have probably been due to excitation or stimulation of the motory or sensory commissural fibres which pass beneath them.

As regards the function of the optic lobes, aside from their action as reflex nervous centres for the movements of the iris, there is little to be said, except that they preside over the sense of sight. They are easily reached and operated upon in birds, where they are very large, and their extirpation is followed by total loss of sight, as well as abolition of the reflex movements of the iris. In birds and in those mammals in which they have been operated upon, their action in vision is crossed; *i. e.*, when the lobe is removed upon one side, the sight is lost in the opposite eye, vision in the eye upon the same side being unimpaired. We have long been in the habit, in class-demonstrations, of removing the optic lobe on one side from a pigeon, with the result just mentioned. The operation is quite simple: A part of the skull is removed by the side of one hemisphere, and the optic lobe is seen, in the form of a large, white tubercle, between the posterior portion of the cerebrum and the cerebellum. A little slit is then made in its capsule, and the interior is broken up carefully with a delicate forceps. The animal generally recovers from the operation, blinded in the eye upon the opposite side. In removing the portion of the skull, it is well not to go too far back, as there is then danger of wounding the great venous sinus and complicating the operation by hæmorrhage.

In treating of the special sense of sight, we shall see that the decussation of the optic nerves is more complex in man than in birds, in which the nerve from one optic lobe passes totally and exclusively to the eye upon the opposite side. In man, most of the fibres of the optic nerve from one side pass to the eye upon the opposite side; but a few fibres pass to the eye upon the same side, a few connect the tubercles upon the two sides, and a few connect the two eyes. It is not known whether or not, in man, the action of the tubercles in vision is exclusively crossed, as it appears to be in most of the inferior animals.

The optic lobes undoubtedly serve as the sole centres presiding over the sense of sight, and not merely as avenues of communication of this sense to the cerebral hemispheres. A positive proof of this proposition lies in the fact that the sense of sight is preserved after complete removal of the cerebrum, provided that injury of the tubercles have been carefully avoided.

We shall say nothing, in this connection, with regard to the movements of the iris, except that the reflex action by which the size of the pupil is modified is effected through the optic lobes as nerve-centres. The mechanism of the movements of the iris and their regulation through nervous action are questions of great interest and are somewhat complex. We have already treated of them to some extent, in connection with the physiology of the third pair of nerves, and they will be considered still more fully in the section upon the special sense of sight.

Ganglion of the Tuber Annulare.

The tuber annulare, called the pons Varolii or the mesocephalon, is situated at the base of the brain, just above the medulla oblongata. It is white externally and contains in its interior a large admixture of gray matter. It presents both transverse and longitudinal white fibres. Its transverse fibres connect the two halves of the cerebellum. Its longitudinal fibres are connected below, with the anterior pyramidal bodies and the olivary bodies of the medulla oblongata, the lateral columns of the cord, and a certain portion of the posterior columns. Above, the fibres are connected with the crura cerebri and pass to the brain. The superficial transverse fibres are wanting in animals in which the cerebellum has no lateral lobes.

The general properties of the tuber annulare have been demonstrated in the most satisfactory manner by Longet. In his experiments, direct excitation of the superficial transverse fibres did not produce well-marked convulsive movements, and there were no convulsions when the posterior fibres were stimulated. When galvanization was applied to the deeper anterior fibres, convulsive movements were distinct at each excitation. Stimulation of the posterior portion always produced pain. This was not constantly observed to follow irritation of the anterior portion, and, when pain occurred, it was thought to be due to irritation of the root of the fifth nerve.

The above experiments, it is true, are not so free from uncertainty as those made upon the more accessible parts of the encephalon, but, as far as they go, they tend to show that the tuber annulare is both insensible and inexcitable in its superficial anterior portion, which is composed chiefly of commissural fibres from the cerebellum; that it is excitable and probably insensible in its deeper anterior portion, which seems to be composed chiefly of descending motor conductors; and, finally, that it is sensible and probably inexcitable in its posterior portion.

The tuber annulare undoubtedly acts as a conductor of sensory impressions and motor stimulus to and from the cerebrum, as we should naturally expect from the direction of its fibres, and as has been repeatedly shown by cases of disease, particularly as regards motion. In addition, however, judging from the fact that it contains numerous nodules of gray matter between fasciculi of white fibres, and that this gray matter contains cellular elements similar to those found in other nerve-centres and from which nerve-fibres undoubtedly originate, it would be inferred that these nodules have a distinct function and give to the tuber annulare the properties of a nerve-centre. It will be interesting, therefore, to follow out the experiments upon this part, by which its action as a centre has been illustrated. These experiments are of two kinds: First, the removal of other encephalic ganglia, leaving only the tuber annulare, the medulla oblongata, and the cerebellum, and noting the properties or faculties retained by animals under these conditions. Experiments of this kind are tolerably definite, as we already know the general functions of most of the other encephalic ganglia. Second, to note the effects of extirpation of the tuber annulare alone.

If the cerebral hemispheres, the olfactory ganglia, the optic lobes, the corpora striata, and the optic thalami, be removed, the animal loses the special senses of smell and sight and the intellectual faculties, there is a certain amount of enfeeblement of the muscular system, but voluntary motion and general sensibility are retained. There can be no doubt upon these points. As far as voluntary motion is concerned, an animal operated upon in this way is in nearly the same condition as one simply deprived of the cerebral hemispheres. There are no voluntary movements which show any degree of intelligence, but the animal can stand, and various consecutive movements are executed, which are entirely different from the simple reflex acts depending exclusively upon the spinal cord. The coördination of movements is perfect, unless the cerebellum be removed. As regards general sensibility, an animal deprived of all the encephalic ganglia except the tuber annulare and the medulla oblongata undoubtedly feels pain. This has been demonstrated in the most conclusive manner by Longet, and has been shown even more satisfactorily by Vulpian. In rabbits, rats, etc., after removal of the cerebrum, corpora striata, and optic thalami, pinching of the ear or foot is immediately followed by prolonged and plaintive cries. Both of the experimenters referred to insist upon the character of these cries as indicating the actual perception of painful impressions, and as very different from cries that are purely reflex, according to the ordinary acceptation of this term. Longet alludes to the voluntary movements and the cries observed in persons subjected to painful surgical operations, when incompletely under the influence of an anæsthetic, concerning the character of which there can be no doubt. He regards the movements as voluntary, and the cries as evidence of the acute perception of pain; but it is well known that such patients have no recollection of any painful impression, although they have apparently experienced great suffering. As far as we can judge from what we positively know of the functions of the encephalic centres, the pain under these circumstances is perceived by some nerve-centre, probably the tuber annulare, but the impression is not conveyed to the cerebrum and is not recorded by the memory.

Taking all the experimental facts into consideration, the following seems to be the most reasonable view with regard to the function of the tuber annulare as a nerve-centre:

It is an organ capable of originating a stimulus giving rise to voluntary movements, when the cerebrum, corpora striata, and the optic thalami, have been removed, and it probably regulates the automatic voluntary movements of station and progression. Many voluntary movements, the result of intellectual effort, are made in obedience to a stimulus transmitted from the cerebrum, through conducting fibres in the tuber annulare, to the motor conductors of the cord and the general motor nerves.

The tuber annulare is also capable of perceiving painful impressions, which, when all of the encephalic ganglia are preserved, are also conducted to and are perceived by the cerebrum, and are remembered; but there are distinct evidences of the perception of pain, even when the cerebrum has been removed.

Medulla Oblongata.

The chief points of interest in the physiological anatomy of the medulla oblongata relate to the direction of its fibres, their connection with the gray matter embedded in its substance, and the course of the filaments of origin of certain of the cranial nerves. Concerning the deep origin of the large root of the fifth, the motor oculi externus, facial, pneumogastric, spinal accessory, and the sublingual, we shall have nothing to say in this connection, as we have already treated of the physiological anatomy of these nerves with sufficient minuteness; and we have now to study the functions of the medulla oblongata, and particularly its action as a nerve-centre.

Physiological Anatomy of the Medulla Oblongata.—The medulla oblongata is the oblong enlargement which connects the spinal cord with the various encephalic ganglia. It is about an inch and a quarter in length, and nearly an inch broad at its widest portion. It rests in the basilar groove of the occipital bone, extending from the atlas to the lower border of the tuber annulare, with its broad extremity above. Like the cord, it has an anterior and a posterior median fissure.

Apparently continuous with the anterior columns of the cord, are the two anterior pyramids, one on either side. Viewed superficially, the innermost fibres of these pyramids are seen to decussate in the median line; but, if these fibres be traced from the cord, it is found that they come from the white substance of its lateral columns, and that none of them are derived from the anterior columns. The fibres of the external portion of the anterior pyramids come from the anterior columns of the cord. At the site of the decussation, the pyramids are composed entirely of white matter; but, as the fibres spread out to pass to the encephalon above, they present nodules of gray matter between the fasciculi.

External to the anterior pyramids, are the corpora olivaria. These are oval and are surrounded by a distinct groove. They are white externally and contain a gray nucleus, called the corpus dentatum.

External to the corpora olivaria, are the restiform bodies, formed exclusively of white matter and constituting the postero-lateral portion of the medulla. They are continuous with the posterior columns of the cord. The restiform bodies spread out as they ascend, and pass to the cerebellum, forming a great portion of the inferior peduncles.

Beneath the olivary bodies and between the anterior pyramids and the restiform bodies, are the lateral tracts of the medulla, called by the French, the intermediary fasciculi. These are composed of an intimate mixture of white and gray matter and have a yellowish-gray color. They receive all that portion of the antero-lateral columns of the cord which does not enter into the composition of the anterior pyramids. They are frequently considered as parts of the restiform bodies, but they are peculiarly interesting, from the fact that they contain the gray centre presiding over respiration; and, for that reason, we have described them as distinct fasciculi.

The posterior pyramids (fasciculi graciles) are the smallest of all. They pass upward to the cerebrum, without decussating, and are composed exclusively of white matter. As they pass upward, they diverge, leaving a space at the fourth ventricle.

The fourth ventricle is in the medulla, and is bounded above, by the valve of Vieussens and the under surface of the cerebellum. In the lower part of the floor of the fourth ventricle, are several transverse fasciculi of white matter; but the greatest part of this portion is composed of a layer of gray substance.

The two lateral halves of the posterior portion of the medulla are connected together by fibres arising from the gray matter of the lateral tracts, or intermediary fasciculi, passing obliquely, in a curved direction from behind forward, to the raphe in the median line. There are also fibres passing from before backward, to form a posterior commissure, and fibres arising from the cells of the olivary bodies, which connect the gray substance of the lateral halves. Commissural fibres also connect the gray matter of the lateral tracts with the corpora dentata of the olivary bodies, and the olivary bodies with the cerebellum, their fibres forming part of the inferior peduncles of the cerebellum. In addition, it is probable that fibres, taking their origin from all of the gray nodules of the medulla, pass to the parts of the encephalon situated above.

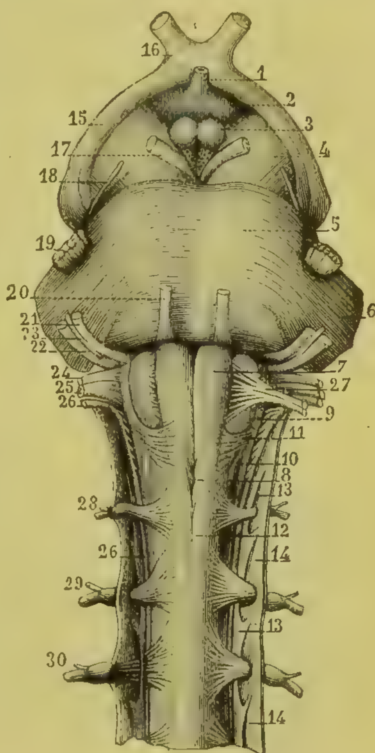


FIG. 229.—*Anterior view of the medulla oblongata.* (Sappey.)

1, infundibulum; 2, tuber cinereum; 3, corpora albicantia; 4, cerebral peduncle; 5, tuber annulare; 6, origin of the middle peduncle of the cerebellum; 7, *anterior pyramids of the medulla oblongata*; 8, *decussation of the anterior pyramids*; 9, *olivary bodies*; 10, *restiform bodies*; 11, *arciform fibres*; 12, upper extremity of the spinal cord; 13, ligamentum denticulatum; 14, 14, dura mater of the cord; 15, optic tracts; 16, chiasm of the optic nerves; 17, motor oculi communis; 18, patheticus; 19, fifth nerve; 20, motor oculi externus; 21, facial nerve; 22, auditory nerve; 23, nerve of Wrisberg; 24, glosso-pharyngeal nerve; 25, pneumogastric; 26, 26, spinal accessory; 27, sublingual nerve; 28, 29, 30, cervical nerves.

As far as the fibres of origin of the nerves are concerned, it may be stated in general terms that a number of the motor roots arise from the gray matter of the floor of the fourth ventricle, the roots of the sensory nerves arising from gray matter in the posterior portions.

Aside from purely anatomical demonstrations, the connection of the anterior pyramids of the medulla with the corpora striata has been shown by pathological observations. It is well known that, when the connection between the nerve-centres and the fibres is destroyed, these fibres after a time become degenerated. In old lesions of the corpora striata, it has been shown that, when the white substance is injured upon one side, there follow degeneration and atrophy of the fibres of the corresponding cerebral peduncle and anterior pyramid of the medulla, and of the lateral portion of the spinal cord upon the opposite side. This important fact illustrates the connection between the lateral columns of the cord and the anterior pyramids of the medulla oblongata, the decussation of the anterior pyramids, and the passage of fibres from the anterior pyramids to the corpora striata, in the substance of the cerebral peduncles.

Functions of the Medulla Oblongata.

It is hardly necessary to discuss the functions of the medulla oblongata as a conductor of sensory impressions and of motor stimulus to and from the brain. We know that there is conduction of this kind from the spinal cord to the ganglia of the encephalon, and this must take place through the medulla; a fact which is inevitable, from its anatomical relations, and which is demonstrated by its section in living animals. Nor is it necessary to dwell upon its general properties, in which it resembles the spinal cord, at least as far as has been demonstrated by experiments upon living animals or upon animals just killed. It is difficult to expose this part in the higher classes of animals, but experiments show that it is sensitive on its posterior surface and insensible in front. The difficulty of observing the phenomena which follow its irritation in living animals has rendered it impossible to determine the limits of its excitability and sensibility as exactly as has been done for the different portions of the cord.

It is also somewhat difficult to determine whether the action of the medulla itself, in its relations to motion and sensation, be crossed or direct. As regards conduction from the brain, the direction is sufficiently well shown by cases of cerebral disease, in which the paralysis, in simple lesions, is always on the opposite side of the body.

The action of the medulla as a reflex nerve-centre depends upon its gray matter. When this gray substance is destroyed, certain of the important reflex functions are instantly abolished. From its connections with various of the cranial nerves, we should expect it to play an important part in the movements of the face, in deglutition, in the action of the heart and of various glands, etc., important points which will be fully considered in their appropriate place. Its most striking function, however, is in connection with respiration.

Connection of the Medulla Oblongata with Respiration.—In 1809, Legallois made a number of experiments upon rabbits, cats, etc., in which he showed that respiration depends exclusively upon the medulla oblongata and not upon the brain, and he farther located the part which presides over this function at the site of origin of the pneumogastric nerves. Flourens, in his elaborate experiments upon the nerve-centres, extended the observations of Legallois, and limited the respiratory centre in the rabbit, between the upper border of the roots of the pneumogastrics and a plane situated about a quarter of an inch below the lowest point of origin of these nerves; these limits, of course, varying with the size of the animal. Following these experiments, Longet has shown that the respiratory nervous centre does not occupy the whole of the medulla included between the two planes indicated by Flourens, but that it is confined to the gray matter of the lateral tracts, or the intermediary fasciculi. This was demonstrated by the fact that respiration persists in animals after division of the anterior pyramids and the restiform bodies. Subsequently, Flourens still farther restricted the limits of the respiratory centre and fully confirmed the observations of Longet.

The portion of the medulla oblongata above indicated presides over the movements of respiration and is the true respiratory nerve-centre. Nearly all who have repeated the experiments of Flourens have found that the spinal cord may be divided below the medulla oblongata, and that all of the encephalic ganglia above may be removed, respiratory movements still persisting. It is a very common thing in vivisections to kill an animal by breaking up the medulla. In a dog, for example, we grasp the head firmly with the left hand, flex it forcibly upon the neck, and penetrate with a stylet a little behind the occipital protuberance, entering between the atlas and the skull. By a rapid lateral motion of the instrument, the medulla is broken up, and the animal instantly ceases to breathe. There are no struggles, no manifestations of the distress of asphyxia; the respiratory muscles simply cease their action, and the animal loses instantly the sense of want of air. A striking contrast to this is presented when the trachea is tied or when all of the respiratory muscles are paralyzed without touching the medulla.

FIG. 230. — *Stylet for breaking up the medulla oblongata.* (Bernard.)

In another chapter, we have insisted upon the mechanism of the reflex phenomena of respiration. We have conclusively shown by experiments, that an impression is received by the sensory nerves of the general system, which is due to want of oxygen and not to the irritation produced by carbonic acid; and that this impression is conveyed to the medulla oblongata and gives rise to the reflex movements of respiration. If this impression be abolished, there are no respiratory movements; and if the medulla, the sole centre capable of receiving this impression and of generating the stimulus sent to the respiratory muscles, be destroyed, respiration instantly ceases, without any sensation of asphyxia.

Vital Point (*so called*).—Since it has been definitely ascertained that destruction of a restricted portion of the gray substance of the medulla produces instantaneous and permanent arrest of the respiratory movements, Flourens and others have spoken of this centre as the vital knot, destruction of which is immediately followed by death. With our present knowledge of the properties and functions of the different tissues and organs of which the body is composed, it is almost unnecessary to present any arguments to show the unphilosophical character of such a sweeping proposition. We can hardly imagine such a thing as instantaneous death of the entire organism; still less can it be assumed that any restricted portion of the nervous system is the one essential, vital point. Probably, a very powerful electric discharge passed through the entire cerebro-spinal axis produces the nearest approach to instantaneous death of any thing of which we have any knowledge; but, even here, it is by no means certain that some parts do not for a time retain their so-called vital properties. In apparent death, the nerves and the heart may be shown to retain their characteristic properties; the muscles will contract under stimulus, and will appropriate oxygen and give off carbonic acid, or respire; the glands may be made to secrete, etc.; and no one can assume that, under these conditions, the entire organism is dead. We really know of no such thing as death, except as the various tissues and organs which go to make up the entire body become so altered as to lose their physiological properties beyond the possibility of restoration; and this never occurs for all parts of the organism in an instant. A person drowned may be to all appearances dead, and would certainly die without measures for restoration; yet, in such instances, restoration may be accomplished, the period of apparent death being simply a blank, as far as the recollection of the individual is concerned. It is as utterly impossible to determine the exact instant when the vital principle, or whatever it may be called, leaves the body in death, as to indicate the time when the organism becomes a living being. Death is nothing more than a permanent destruction of so-called vital physiological properties; and this occurs successively, and at different periods, for different tissues and organs.

When we see that frogs will live for weeks, and sometimes for months, after destruction of the medulla oblongata, and that, in mammals, by keeping up artificial respiration, we can prolong many of the most important functions, as the action of the heart, for hours after decapitation, we can understand the physiological absurdity of the proposition that there is any such thing as a vital point, in the medulla or in any part of the nervous system.

Connection of the Medulla Oblongata with Various Reflex Acts.—There are numerous reflex phenomena that are completely under the control of the medulla oblongata as a nerve-centre. Among these are the various acts connected with respiration, as yawning, coughing, crying, sneezing, etc. It also presides over the coördination of the muscles concerned in expression, and the act of vomiting. We have seen, in treating of the pneumogastric nerves, that their galvanization arrests the action of the heart in diastole. The same result follows galvanization of the medulla at the point of origin of these nerves. We have also fully discussed the influence of the medulla upon sugar-formation in the liver, as illustrated by the striking experiments of Bernard, in which he produced diabetes in animals by irritating the floor of the fourth ventricle, and the influence of this centre upon the quantity and the composition of the urine.

There is very little to be said concerning certain ganglia and other parts of the brain that we have not yet considered. The olfactory bulbs, or ganglia, preside over olfaction and will be treated of fully in connection with the special senses. The pineal gland and the pituitary body, in their structure, present a certain resemblance to the ductless glands, and their anatomy has been considered in another chapter. Passing over the purely theoretical views of the older writers, who had very indefinite ideas of the functions of any of the encephalic ganglia, we have only to say that the uses of the pineal gland and pituitary body in the economy are entirely unknown. The same remark applies to the corpus callosum, the septum lucidum, the ventricles, hippocampi, and various other minor parts that are necessarily described in anatomical works. It is useless to discuss the early or even the recent speculations with regard to the functions of these parts, which are entirely unsupported by experimental or pathological facts and which have not advanced our positive knowledge. Most of the parts just enumerated have no physiological history.

Rolling and Turning Movements following Injury of Certain Parts of the Encephalon.

The remarkable movements of rolling and turning, produced by section or injury of certain of the commissural fibres of the encephalon, are not very important in their bearing upon the functions of the brain, and they are rather to be classed among the curiosities of experimental physiology. These movements follow unilateral lesions and are dependent, to a certain extent, upon a consequent inequality in the power of the muscles on one side, without actual paralysis. Vulpian enumerates the following parts, injury of which, upon one side, in living animals, may determine movements of rotation:

"1. Cerebral hemispheres;

"2. Corpora striata;

"3. Optic thalami (Flourens, Longet, Schiff);

"4. Cerebral peduncles (Longet);

"5. Pons Varolii;

"6. Tubercula quadrigemina or bigemina (Flourens);

"7. Peduncles of the cerebellum, especially the middle, and the lateral portions of the cerebellum (Magendie);

"8. Olivary bodies, restiform bodies (Magendie);

"9. External part of the anterior pyramids (Magendie);

"10. Portion of the medulla from which the facial nerve arises (Brown-Séquard);
"11. Optic nerves;
"12. Semicircular canals (Flourens); auditory nerve (Brown-Séquard)."

To the parts above enumerated, Vulpian adds the upper part of the cervical portion of the spinal cord.

The movements which follow unilateral injury of the parts mentioned above are of two kinds; viz., rolling of the entire body on its longitudinal axis, and turning, always in one direction, in a small circle, called by the French the movement of *manége*. A capital point to determine in these phenomena is, whether these movements be due to paralysis or enfeeblement of certain muscles upon one side of the body, to a direct or reflex irritation of the parts of the nervous system involved, or to both of these causes combined. The experiments of Brown-Séquard and others conclusively show that the movements may be due to irritation alone, for they occur when parts of the encephalon and the upper portions of the cord are simply pricked, without section of fibres. When there is extensive division of fibres, it is probable that the effects of the enfeeblement of certain muscles are added to the phenomena produced by simple irritation. The most satisfactory explanation of these movements is the one proposed by Brown-Séquard, who attributes them to a more or less convulsive action of muscles on one side of the body, produced by irritation of the nerve-centres. He regards the rolling as simply an exaggeration of the turning movements, and places both in the same category.

We do not propose to enter into an elaborate discussion of the above experiments, for the reason that they do not seem to have advanced our positive knowledge of the functions of the nerve-centres. In some of them, the movements have been observed toward the side operated upon, and in others, toward the sound side. These differences probably depend upon the fact that, in certain experiments, the fibres are involved before their decussation, and in others, after they have crossed in the median line. In some instances, the movements may be due to a reflex action, from stimulation of afferent fibres, and in others, the action of the irritation may be direct. Judging from the fact that most of the encephalic commissural fibres are apparently insensible and inexcitable under direct stimulation, it is probable that the action is generally reflex.

In concluding the physiological history of the encephalon, we have only to refer to the general properties of certain of the peduncles. Longet found that direct irritation of the superior and the inferior peduncles of the cerebellum, in rabbits, produced pain, but the disturbance consequent upon exposure of the parts did not allow of any accurate observations upon the movements. He says nothing of the general properties of the middle peduncles or of the peduncles of the cerebrum.

CHAPTER XXII.

SYMPATHETIC NERVOUS SYSTEM—SLEEP.

General arrangement of the sympathetic system—Peculiarities in the intimate structure of the sympathetic ganglia and nerves—General properties of the sympathetic ganglia and nerves—Functions of the sympathetic system—Vaso-motor nerves—Reflex phenomena operating through the sympathetic system—Trophic centres and nerves (so called)—Sleep—General considerations—Condition of the organism during sleep—Dreams—Reflex mental phenomena during sleep—Condition of the brain and nervous system during sleep—Theories of sleep—Anæsthesia and sleep produced by pressure upon the carotid arteries—Differences between natural sleep and stupor or coma—Regeneration of the brain-substance during sleep—Theory that sleep is due to a want of oxygen—Condition of the various functions of the organism during sleep.

WHILE there are certain points in the physiology of the sympathetic nervous system that are perfectly well established, it must be admitted that its functions are, in many respects, obscure, and that our positive knowledge of its general properties and its relations to the functions of nutrition, secretion, movements, etc., amounts to comparatively little. The very name, sympathetic, is some indication of our indefinite ideas with regard to its functions; but we have adopted this name, for the reason that it is the one most generally in use, although it has no very exact relation to the peculiar functions of the system. It is sometimes called the ganglionic nervous system; but this name is inappropriate, as it implies that it alone possesses ganglia. The name of the system of organic, or vegetative life is more in accordance with its general functions; but this is not so commonly used as that of sympathetic system. The older anatomists and physiologists called the great cord of this system the nervus intercostalis.

As far as we know, there is no account of the sympathetic system, even in the most recent works upon physiology or in special treatises, a careful study of which does not convey the idea that there is little else in the literature of the subject than controversial questions of priority, etc., in minor details, and a few observations, some of them quite unsatisfactory, with regard to the effects of the division or galvanization of sympathetic filaments upon the functions of circulation, secretion, and animal heat. It is unfortunate that well-ascertained facts, which might be stated in a very few pages, should be so largely overshadowed by a mass of purely historical details of no great interest. Still, we must take the physiological data as we find them and endeavor not to limit the knowledge to be looked for in the future, by adopting theories upon insufficient positive evidence.

There are certain important anatomico-physiological questions, more or less definitely determined, that have a direct bearing upon the functions of the sympathetic system. These are the following: Is the sympathetic anatomically and physiologically dependent upon its connections with the cerebro-spinal nerves? What are the general properties of the sympathetic nerves as regards motion and sensation? Do the sympathetic ganglia act as independent reflex nerve-centres? To what extent and in what way do the sympathetic ganglia and nerves influence the functions of the various organs and tissues to which their filaments are distributed? A solution of these questions involves a careful and critical study of the results of experiments upon living animals and of pathological facts; and it is evident that very little information is to be derived from observations made anterior to the discovery of the properties and functions of the most important parts of the cerebro-spinal system. We shall begin the study of these points with an account of the general arrangement and the peculiarities of structure of the sympathetic ganglia and nerves.

General Arrangement of the Sympathetic System.

Like the cerebro-spinal system, the sympathetic is composed of centres and nerves, at least as far as we can judge from its anatomy. The centres contain nerve-cells, most of which differ but little from the cells of the encephalon and spinal cord. The nerves are composed of fibres, the greater part of which are nearly identical in structure with the ordinary motor and sensory fibres. The fibres are connected with the nerve-cells in the ganglia, and the ganglia are connected with each other by commissural fibres. These ganglia constitute a continuous double chain, on either side of the body, beginning above, by the ophthalmic ganglia, and terminating below, in the ganglion impar. It is important to note, however, that the chain of sympathetic ganglia is not independent, but that each ganglion receives motor and sensory filaments from the cerebro-spinal nerves, and that some filaments pass from the sympathetic to the cerebro-spinal system. The general distribution of the sympathetic filaments is to mucous membranes—and possibly to integument—to non-striated muscular fibres, and particularly to the muscular coat of the arteries. As far as we have been able to learn from anatomical investigations, there are no fibres derived exclusively from the sympathetic which are distributed to striated muscles, except those which pass to the muscular tissue of the heart. Near the terminal filaments of the sympathetic, in most of the parts to which these fibres are distributed, there exist numerous ganglionic cells.

The general arrangement of the sympathetic ganglia and the distribution of the nerves may be stated, sufficiently for our purposes, very briefly; still, a knowledge of certain anatomical points is indispensable as an introduction to an intelligent study of the physiology of this system.

In the cranium, are four ganglia; the ophthalmic, the spheno-palatine, the otic, and the submaxillary. In the neck, are the three cervical ganglia; the superior, middle, and inferior. In the chest, are the twelve thoracic ganglia, corresponding to the twelve ribs. The great semilunar ganglia, the largest of all, sometimes called the abdominal brain, are in the abdomen, by the side of the cœliac axis. In the lumbar region, in front of the spinal column, are the four, and sometimes five, lumbar ganglia. In front of the sacrum, are the four or five sacral, or pelvic ganglia; and in front of the coccyx, is a small, single ganglion, the last of the chain, called the ganglion impar. Thus, the sympathetic cord, as it is sometimes called, consists of from twenty-eight to thirty ganglia on either side, terminating below in a single ganglion.

Cranial Ganglia.—The ophthalmic, lenticular, or ciliary ganglion is situated deeply in the orbit, is of a reddish color, and about the size of a pin's-head. It receives a motor branch from the third pair, and sensory filaments from the nasal branch of the ophthalmic division of the fifth. It is also connected with the cavernous plexus and with Meckel's ganglion. Its so-called motor and sensory roots from the third and the fifth pair have already been described in connection with these nerves. Its filaments of distribution are the ten or twelve short ciliary nerves, which pass to the ciliary muscle and the iris. A very delicate filament from this ganglion passes to the eye with the central artery of the retina, in the canal in the centre of the optic nerve.

The functions of the ophthalmic ganglion are connected exclusively with the action of the ciliary muscle and iris; and we shall here merely indicate its anatomical relations, leaving its physiology to be taken up under the head of vision.

The spheno-palatine ganglion was first described by Meckel and is known as Meckel's ganglion. This is the largest of the cranial ganglia. It is of a triangular shape, reddish in color, and is situated in the spheno-maxillary fossa, near the spheno-palatine foramen. It receives a motor root from the facial, by the Vidian nerve. Its sensory roots are the two spheno-palatine branches from the superior maxillary division of the fifth. Its branches of distribution are quite numerous. Two or three delicate filaments enter the orbit and go to its periosteum. Its other branches, which it is unnecessary to describe fully in detail, are distributed to the gums, the membrane covering the hard palate, the soft palate, the uvula, the roof of the mouth, the tonsils, the mucous membrane of the nose, the middle auditory meatus, a portion of the pharyngeal mucous membrane, and the levator palati and azygos uvulæ muscles. It is probable that the filaments sent to these two striated muscles are derived from the facial nerve and do not properly belong to the sympathetic system. The ganglion also sends a short branch, of a reddish-gray color, to the carotid plexus.

The otic ganglion, sometimes called Arnold's ganglion, is a small, oval, reddish-gray mass, situated just below the foramen ovale. It receives a motor filament from the facial, and sensory filaments from branches of the fifth and the glosso-pharyngeal. Its filaments of distribution go to the mucous membrane of the tympanic cavity and Eustachian tube and to the tensor tympani and tensor palati muscles. Reasoning from the general mode of distribution of the sympathetic filaments, those going to the striated muscles are derived from the facial. It also sends branches to the carotid plexus.

The submaxillary ganglion, situated on the submaxillary gland, is small, rounded, and of a reddish-gray color. It receives motor filaments from the chorda tympani and sensory filaments from the lingual branch of the fifth. Its filaments of distribution go to Wharton's duct, to the mucous membrane of the mouth, and to the submaxillary gland.

Cervical Ganglia.—The three cervical ganglia are situated opposite the third, fifth,

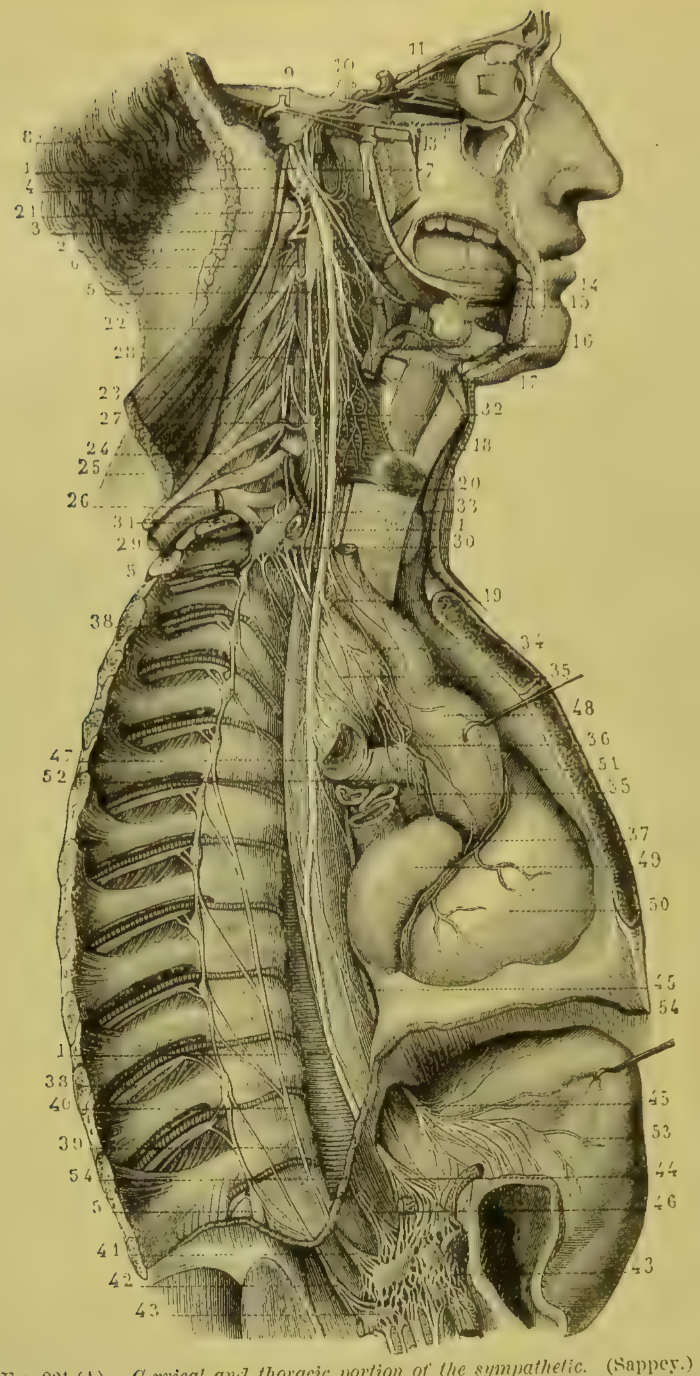


FIG. 231 (A).—*Cervical and thoracic portion of the sympathetic.* (Sappey.)

1, 1, 1, right pneumogastric; 2, glosso-pharyngeal; 3, spinal accessory; 4, divided trunk of the sublingual;
5, 5, 5, *chain of ganglia of the sympathetic*; 6, *superior cervical ganglion*; 7, *branches from this ganglion to*
the carotid; 8, nerve of Jacobson; 9, *two filaments from the facial, one to the spheno-palatine and the other*
to the otic ganglion; 10, motor oculi externus; 11, *ophthalmic ganglion, receiving a motor filament from*
the motor oculi communis and a sensory filament from the nasal branch of the fifth; 12, *spheno-palatine*
ganglion; 13, *otic ganglion*; 14, lingual branch of the fifth nerve; 15, *submaxillary ganglion*; 16, 17,
superior laryngeal nerve; 18, external laryngeal nerve; 19, 20, recurrent laryngeal nerve; 21, 22, 23,
anterior branches of the upper four cervical nerves, sending filaments to the superior cervical sympathetic
ganglion; 24, *anterior branches of the fifth and sixth cervical nerve, sending filaments to the middle cervical*
ganglion; 25, 26, *anterior branches of the seventh and eighth cervical and the first dorsal nerves, sending fila-*
ments to the inferior cervical ganglion; 27, *middle cervical ganglion*; 28, *cord connecting the two ganglia*;
29, *inferior cervical ganglion*; 30, 31, *filaments connecting this with the middle ganglion*; 32, *superior car-*
diac nerve; 33, *middle cardiac nerve*; 34, *inferior cardiac nerve*; 35, 35, *cardiac plexus*; 36, *ganglion of*
the cardiac plexus; 37, *nerve following the right coronary artery*; 38, 38, *intercostal nerves, with their two*
filaments of communication with the thoracic ganglia; 39, 40, 41, *great splanchnic nerve*; 42, *lesser splanchnic*
nerve; 43, 43, *solar plexus*; 44, left pneumogastric; 45, right pneumogastric; 46, lower end of the phrenic
nerve; 47, section of the right bronchus; 48, arch of the aorta; 49, right auricle; 50, right ventricle; 51,
52, pulmonary artery; 53, right half of the stomach; 54, section of the diaphragm.

and the seventh cervical vertebræ respectively. The middle ganglion is sometimes wanting, and the inferior is occasionally fused with the first thoracic ganglion. These ganglia are connected together by the so-called sympathetic cord. They have numerous filaments of communication above, with the cranial and the cervical nerves of the cerebro-spinal system. Branches from the superior ganglion go to the internal carotid, to form the carotid and the cavernous plexus, following the vessels as they branch to their distribution. Branches from this ganglion pass to the cranial ganglia. There are also branches which unite with filaments from the pneumogastric and the glosso-pharyngeal to form the pharyngeal plexus, and branches which form a plexus on the external carotid, the vertebral, and the thyroid artery, following the ramifications of these vessels.

From the cervical portion of the sympathetic, the three cardiac nerves arise and pass to the heart, entering into the formation of the cardiac plexus. The superior cardiac nerve arises from the superior ganglion; the middle nerve, the largest of the three, arises from the middle ganglion, or from the sympathetic cord, when this ganglion is wanting; and the inferior nerve arises from the inferior cervical ganglion or the first thoracic. These nerves present numerous communications with various of the adjacent cerebro-spinal nerves, penetrate the thorax, and form the deep and the superficial cardiac plexus and the posterior and the anterior coronary plexus. In these various plexuses, are found numerous ganglioform enlargements; and, upon the surface and in the substance of the heart, are numerous collections of nerve-cells connected with the fibres.

Thoracic Ganglia.—The thoracic ganglia are situated in the chest, beneath the pleura, and rest on the heads of the ribs. They are usually twelve in number, but occasionally two are fused into one. They are connected together by the sympathetic cord. They each communicate by two filaments with the cerebro-spinal nerves. One of these is white, like the spinal nerves, and probably passes to the sympathetic, and the other, of a grayish color, is thought to contain the true sympathetic filaments. From the upper six ganglia, filaments pass to the aorta and its branches. The branches which form the posterior pulmonary plexus arise from the third and fourth ganglia. The great splanchnic nerve arises mainly from the seventh, eighth, and ninth ganglia, receiving a few filaments from the upper six ganglia. This is a large, white, rounded cord, which penetrates the diaphragm and passes to the semilunar ganglion, sending a few filaments to the renal plexus and the suprarenal capsules. The lesser splanchnic nerve arises from the tenth and eleventh ganglia, passes into the abdomen, and joins the cœliac plexus. The renal splanchnic nerve arises from the last thoracic ganglion and passes to the renal plexus. The three splanchnic nerves present numerous anastomoses with each other.

Ganglia in the Abdominal and the Pelvic Cavity.—The semilunar ganglia on the two sides send off radiating branches to form the solar plexus. They are situated by the side of the cœliac axis and near the suprarenal capsules. These are the largest of the sympathetic ganglia. From these arise numerous plexuses distributed to various parts in the abdomen, as follows: The phrenic plexus follows the phrenic artery and its branches to the diaphragm. The cœliac plexus subdivides into the gastric, hepatic, and splenic plexuses, which are distributed to organs as their names indicate. From the solar plexus, different plexuses are given off, which pass to the kidneys, the suprarenal capsules, the testes in the male, and the ovaries in the female, the intestines (by the superior and the inferior mesenteric plexuses), the upper part of the rectum, the abdominal aorta, and the vena cava. The filaments follow the distribution of the blood-vessels in the solid viscera.

The lumbar ganglia, four in number, are situated in the lumbar region, upon the bodies of the vertebræ. They are connected with the ganglia above and below and with each other by the sympathetic cord, receiving, like the other ganglia, filaments from the spinal nerves. Their branches of distribution form the aortic lumbar plexus and the hypogastric plexus and follow the course of the blood-vessels.

The four or five sacral ganglia and the ganglion impar are situated by the inner side of the sacral foramina and in front of the coccyx. These are connected with the ganglia above and with each other, and receive filaments from the sacral nerves, there being

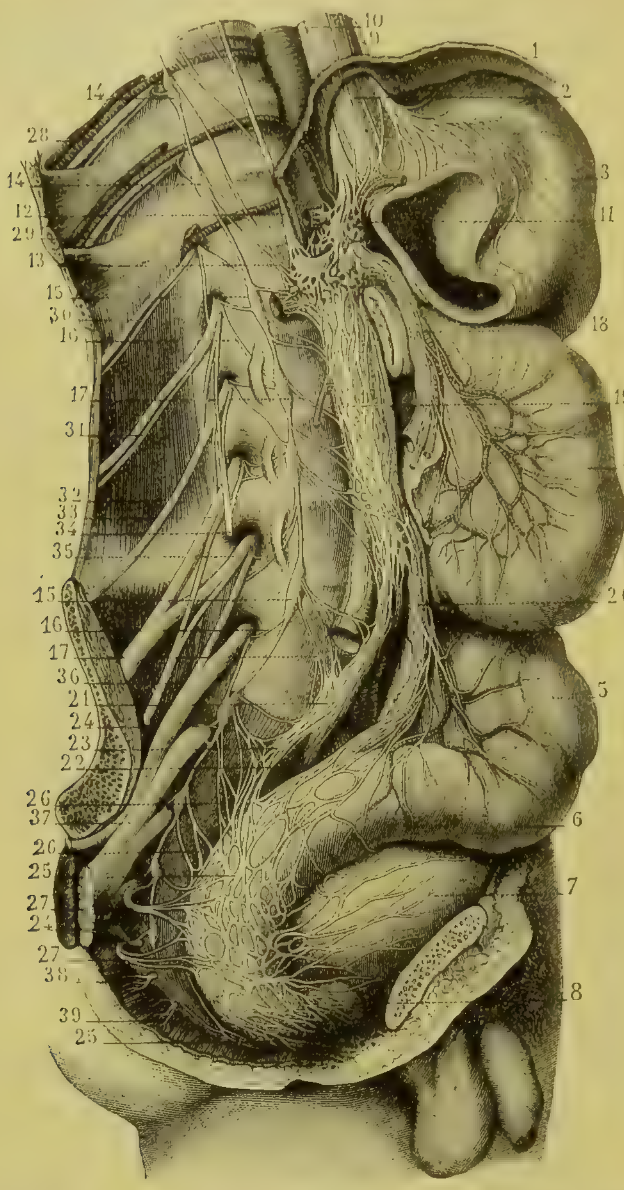


Fig. 231 (B).—*Lumbar and sacral portions of the sympathetic.* (Sappey.)

1, section of the diaphragm; 2, lower end of the œsophagus; 3, left half of the stomach; 4, small intestine; 5, sigmoid flexure of the colon; 6, rectum; 7, bladder; 8, prostate; 9, lower end of the left pneumogastric; 10, lower end of the right pneumogastric; 11, *solar plexus;* 12, *lower end of the great splanchnic nerve;* 13, *lower end of the lesser splanchnic nerve;* 14, 14, *last two thoracic ganglia;* 15, 15, *the four lumbar ganglia;* 16, 16, 17, 17, *branches from the lumbar ganglia;* 18, *superior mesenteric plexus;* 19, 21, 22, 23, *aortic lumbar plexus;* 20, *inferior mesenteric plexus;* 24, 24, *sacral portion of the sympathetic;* 25, 25, 26, 26, 27, 27, *hypogastric plexus;* 28, 29, 30, tenth, eleventh, and twelfth dorsal nerves; 31, 32, 33, 34, 35, 36, 37, 38, 39, lumbar and sacral nerves.

generally two branches of communication for each ganglion. The filaments of distribution go to all of the pelvic viscera and the blood-vessels. The inferior hypogastric, or pelvic plexus is a continuation of the hypogastric plexus above, and receives a few filaments from the sacral ganglia. The most interesting branches from this plexus are the uterine nerves, which go to the uterus and the Fallopian tubes. In the substance of the uterus, the nerves are connected with small collections of ganglionic cells. The sympathetic filaments are undoubtedly prolonged into the upper and lower extremities, following the course of the blood-vessels and distributed to their muscular coat.

According to the latest researches, the filaments of the sympathetic, at or near their termination, are connected with ganglionic cells, not only in the heart and the uterus, but in the blood-vessels, lymphatics, coccygeal gland, the submucous and the muscular layer of the entire alimentary canal, the salivary glands, pancreas, excretory ducts of the liver and pancreas, the larynx, trachea, pulmonary tissue, bladder, ureters, the entire generative apparatus, suprarenal capsules, thymus, lachrymal canals, ciliary muscle, and the iris. In these situations, nerve-cells have been demonstrated by various observers, and it is probable that they exist everywhere in connection with the terminal filaments of this system of nerves.

Peculiarities in the Intimate Structure of the Sympathetic Ganglia and Nerves.—The peculiarities in the structure of the cells and fibres of the sympathetic system are not numerous, nor do they possess very great physiological importance. The free communications between the sympathetic ganglia and the cerebro-spinal nerves, and the differences in the general appearance of certain of these anastomosing branches, lead to the important question of their origin. As a rule, the sympathetic nerves are softer and more grayish in color than the spinal nerves. When there are two branches of communication between a ganglion and a spinal nerve, one of them is white and the other is grayish, and we might infer from this that one, the white, is derived from the spinal system, and the other, from the sympathetic; but this is a point not yet settled by microscopical investigations. It has been conclusively shown, however, that the communicating fibres pass in both directions.

While the branches of the sympathetic contain a large number of the ordinary medullated fibres, such as are found in the cerebro-spinal nerves, they also present numerous fibres of Remak, and fine fibres, from $\frac{1}{10000}$ to $\frac{1}{5500}$ of an inch in diameter, which are regarded by Kölliker as true efferent fibres from the sympathetic ganglia. With regard to the fibres of Remak, we have nothing to add to what we have already stated under

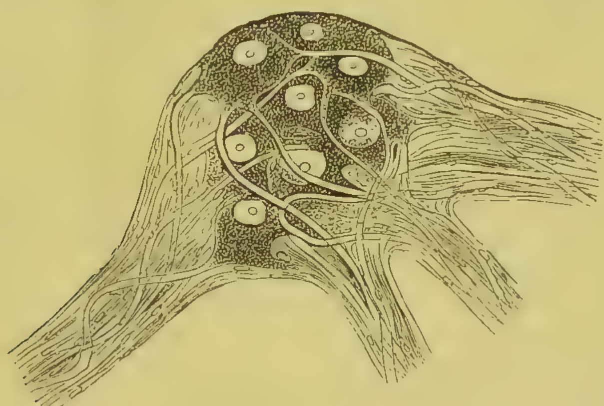


FIG. 232.—*Sympathetic ganglion with multipolar cells; highly magnified.* (Leydig.)

the head of the general structure of the nervous system. These points, with the fact that most of the terminal filaments of the sympathetic are connected with nerve-cells in the substance of the different tissues, constitute the most important anatomical peculiarities of the sympathetic nerve-fibres.

With regard to the cells, which constitute the characteristic anatomical element of the sympathetic ganglia, we shall have little to say, as their peculiarities at present seem to be of purely anatomical interest. They are generally rounded, ovoid, or pear-shaped, with a nucleus, generally clear, and a distinct nucleolus. They present a nucleated capsule, probably composed of connective tissue, which is sometimes lined on its inner surface with a single layer of flattened, polygonal epithelium. Some of the cells are unipolar, some are bipolar, and some are multipolar. In frogs, Beale and Arnold have described a peculiar appearance in certain cells, there being a single, straight prolongation, surrounded by a fine, spiral fibre. These have not been demonstrated in the human subject, and it is not necessary to enter into a discussion of the probable origin and nature of the spiral fibre. The connection between the cells and fibres of the sympathetic is probably the same as in the cerebro-spinal centres and is represented in the accompanying diagram, taken from Leydig. (See Fig. 233.)

General Properties of the Sympathetic Ganglia and Nerves.

The older writers had no definite ideas with regard to the functions of the sympathetic system, and they were divided, even on the simple question of its sensibility, some assuming that the ganglia were absolutely insensible, while others noted distinct evidences of pain following their irritation in living animals. The sensibility of the ganglia, though distinct, is dull as compared with that of the ordinary sensory nerves. We have also noted a dull but well-marked sensibility of the cervical ganglia in rabbits. In view of the decided and uniform results of the most careful recent experiments upon this point, there can be no doubt of the existence of a certain degree of sensibility in the ganglia of the sympathetic system.

As regards excitability, recent experiments are quite satisfactory. Müller exposed the intestines and the semilunar ganglia in rabbits; and, having waited until the intestines, which generally present movements upon first opening the abdomen, had ceased their contractions, the peristaltic movements "were immediately renewed with extraordinary activity" by touching the ganglia with caustic potash. The experiments of Longet show that a feeble continued galvanic current applied to the great splanchnic nerves produces contractions of the muscular coat of the intestines when they contain alimentary matters, but that no contractions occur when they are empty. On the other hand, Pflüger has observed that galvanization of the splanchnic nerves produces a passive condition of the small intestine; that is, arrest of its movements without persistent contractions of its muscular coat. More recently, in a series of very elaborate experiments, by Legros and Onimus, it has been shown that the induced galvanic current applied to the splanchnic nerves does not produce peristaltic movements, but that these movements are excited by the constant current.

Taking into consideration the most reliable direct observations upon the sympathetic ganglia and nerves, the fact that their stimulation induces movements in the non-striated muscles to which they are distributed can hardly be doubted. This action is particularly well marked in the muscular coat of the blood-vessels; but here, the function of the nerves is so important, that it merits special consideration and will be treated of fully under the head of the vaso-motor nerves. The mechanism of these movements, however, is peculiar. The action does not immediately follow the stimulation, as it does in the case of the cerebro-spinal nerves and the striated muscles, but it is induced gradually, beginning a few seconds after the irritation and enduring for a time, and it is more or less tetanic. This mode of action is peculiar to the sympathetic nerves and the non-striated muscular fibres.

When we remember the invariable connection of the sympathetic ganglia with the cerebro-spinal nerves, we see at once the importance of the question of the derivation of the motor and sensory properties of the ganglionic system. Are the sympathetic ganglia independent nerve-centres, or do they derive their properties from the cerebro-spinal system? This question may be satisfactorily answered by two kinds of experimental facts: In the first place, section or irritation of the spinal cord and certain of the encephalic centres is capable of influencing the vaso-motor system, a fact which will be dwelt upon more fully in another connection. In the second place, the experiments of Bernard upon the submaxillary ganglion and its influence on the secretion of the submaxillary gland have demonstrated, in the most conclusive manner, that this ganglion is the centre presiding immediately over the reflex phenomena of secretion by the gland; but it has also been shown that, when all of the connections of the submaxillary ganglion with the cerebro-spinal system are divided, after a few days, this ganglion loses its power as a reflex nervous centre. In the chapters upon secretion, we have given numerous examples of reflex action through the sympathetic system. The experiments just cited from Bernard show that individual ganglia belonging to this system may act independently for a time, but that this action cannot continue indefinitely, after the cerebro-spinal branches have been divided. It remains, however, to apply these experiments to other sympathetic ganglia; but, in the case of the submaxillary, they are very satisfactory, from the facility with which the parts may be operated upon and the certainty with which the ganglion may be separated from its connections with the cerebro-spinal system. As regards the explanation of the final loss of power over the functions of the submaxillary gland, the experiments of Waller seem to have escaped the attention of the eminent physiologist whom we have quoted. There is no experimental fact more conclusively demonstrated than that of the anatomical degeneration and consequent loss of physiological function of nerve-fibres in a few days after they have been separated from their centres of origin. After division of a cerebro-spinal nerve-trunk, the tubes soon lose their anatomical characters and will no longer respond to a galvanic stimulus. In the case of the fibres operating upon the submaxillary gland, the question of their degeneration after division of the cerebro-spinal roots was not submitted to microscopical investigation. If these fibres had undergone the degeneration which has so frequently been observed in experiments upon other nerves, their galvanization would not have produced any effect; which was precisely the result obtained by Bernard. In the absence of direct observations upon this point, it is the most reasonable view to adopt, that the fibres from the cerebro-spinal nerves had lost their function, as a natural consequence of separation from their centres, and that this was the cause of the absence of effect upon the gland following their galvanization. The observation of Bernard shows, however, that filaments may pass to special organs from the cerebro-spinal centres through the sympathetic ganglia.

Functions of the Sympathetic System.

In the early part of the last century (1712 and 1725), Pourfour du Petit demonstrated that the influence of the sympathetic nerve in the neck (the great sympathetic was frequently called the nervus intercostalis) was propagated from below upward toward the head, and not from the brain downward. This may be taken as the starting-point of our definite knowledge of the functions of the sympathetic system, though the experiments of Petit showed only the influence of the cervical portion upon the eye. In 1816, Dupuy removed the superior cervical ganglia in horses, with the effect of producing injection of the conjunctiva, increase of temperature in the ear, and an abundant secretion of sweat upon one side of the head and neck. These experiments showed that the sympathetic has an important influence upon nutrition, calorification, and secretion. In 1851, Bernard repeated the experiments of Pourfour du Petit, dividing the sympathetic in the neck on one side in rabbits, and noted, on the corresponding side of the head and the ear, increased vascularity, and an elevation in temperature, amounting to from 7° to 11° Fahr. This condition of increased heat and vascularity continues for several months after division of the nerve. In 1852, Brown-Séquard repeated these experiments and attributed the elevation of temperature directly to an increase in the supply of blood to the parts affected. He made a most important advance in the history of the sympathetic, by demonstrating that its section paralyzed the muscular walls of the arteries, and, farther, that galvanization of the nerve in the neck caused the vessels to contract. This was the discovery of the vaso-motor nerves, concerning which so much has been written within the past few years, and it belongs without question to Brown-Séquard, who published his observations in August, 1852. A few months later, in the same year, Bernard made analogous experiments and presented the same explanation of the phenomena observed.

The above embraces all that is important with regard to the history of experimental observations upon the sympathetic. It is evident that we could know nothing of the functions of this system before the time of Pourfour du Petit, when the prevailing opinion was that the nerve originated from the encephalon, and that its influence was propagated downward; and writings anterior to the experiments of Bernard and of Brown-Séquard present interesting suggestions and theories, but they contain little that bears upon our positive knowledge.

The important points developed by the first experiments of Bernard and of Brown-Séquard were, that the sympathetic system influences the general process of nutrition, and that many of its filaments are distributed to the muscular coat of the blood-vessels. Before these experiments, it had been shown that filaments from this system influenced the contractions of the muscular coats of the alimentary canal. Leaving, for the present, the action of the vaso-motor nerves, we shall briefly recapitulate some of the facts with regard to the influence of the sympathetic upon animal heat and secretion.

When the sympathetic is divided in the neck, the local increase in temperature is always attended with a very great increase in the supply of blood to the side of the head corresponding to the section. The increased temperature is due to a local exaggeration of the nutritive processes, apparently dependent directly upon the hyperæmia; and it is not probable that there are any nerves to which the name of calorific, as distinguished from vaso-motor, can justly be applied. There are numerous instances in pathology of local increase in temperature attending increased supply of blood to restricted parts. In a recent experiment by Bidder, after excising about half an inch of the cervical sympathetic in a half-grown rabbit, the ear on that side, in the course of about two weeks, became distinctly longer and broader than the other.

The experiment of dividing the sympathetic in the neck, especially in rabbits, is so easily performed, that the phenomena observed by Bernard and Brown-Séquard have been repeatedly verified. We have often done this in class-demonstrations. A very striking experiment is the following, suggested by Bernard: After dividing the sympathetic and exhibiting the increase in the temperature and the vascularity of the ear on one side in the rabbit, if both ears be cut off just above the head with a sharp knife, the artery on the side on which the sympathetic has been divided will frequently send up a jet of blood to the height of several feet, while, on the sound side, the jet is always much less forcible, and it may not be observed at all. This experiment succeeds best in large rabbits.

It is very easy to observe the effects of dividing the sympathetic in the neck, but analogous phenomena have been noted in other parts. Among the most striking of these experiments are those reported by Samuel, who noted an intense hyperæmia of the mucous membrane of the stomach and intestines following extirpation of the cœliac plexus. By comparative experiments, it was shown that this did not result from the peritonitis produced by the operation.

As regards secretion, the influence of the sympathetic is very marked. When the sympathetic filaments distributed to a gland are divided, the supply of blood is very much increased, and an abundant flow of the secretion follows. This point we have already discussed in another chapter, where we have referred particularly to the experiments of Bernard upon the salivary glands. In some recent experiments by Peyrani, it has been shown that the sympathetic has a remarkable influence upon the secretion of urine. When the nerves are galvanized in the neck, the amount of urine and urea is increased, and this increase is greater with the induced than with the constant current. When the sympathetic is divided, the quantity of urine and urea sinks to the minimum.

Dr. Moreau has recently published a series of observations on the influence of the sympathetic nerves upon the secretion of liquid by the intestinal canal, which are peculiarly interesting in their bearing upon the sudden occurrence of watery diarrhœa. In these experiments, the abdomen was opened in a fasting animal, and three loops of intestine, each from four to eight inches long, were isolated by two ligatures. All of the nerves passing to the middle loop were divided, taking care to avoid the blood-vessels. The intestine was then replaced, and the wound in the abdomen was closed with sutures. The next day the animal was killed. The two loops with the nerves intact were found empty, as is normal in fasting animals, and the mucous membrane was dry; but the loop with the nerves divided was found filled with a clear, alkaline liquid, colorless or slightly opaline, which precipitated a few flocculi of organic matter on boiling.

Vaso-Motor Nerves.

The experiments which we have already cited demonstrate beyond a doubt the existence of nerves distributed to the muscular coats of the blood-vessels and capable of regulating their caliber and the quantity of blood sent to different parts. These are the vaso-motor nerves, discovered by Brown-Séquard, in 1852. The importance of nerves apable of regulating what we may call the local circulations is sufficiently apparent. The glands, for example, require at certain times an immense increase in their supply of blood, and the same is probably true of the muscles, brain, and other parts. It has been shown, by direct experiments upon living animals, that local variations in the circulation, independent of the action of the heart, actually take place, and that they are of great importance in special functions; and there are numerous instances of such action, which can only take place through the nervous system. The phenomena of blushing and pallor, from mental emotions, are familiar examples.

There can be no doubt of the fact that the sympathetic branches contain filaments capable of modifying the caliber of the blood-vessels, and that the cerebro-spinal nerves also contain elements possessing analogous properties; but when we reflect upon the extensive anastomoses, in both directions, between the sympathetic and the ordinary motor and sensory nerves, we can appreciate the importance of determining the exact origin and course of these vaso-motor fibres. The first important question is, whether the vaso-motor filaments be derived from the sympathetic ganglia or from the cerebro-spinal centres.

All experiments upon the question just proposed tend to show that the vaso-motor nerves are derived exclusively from the cerebro-spinal system and do not originate in the sympathetic ganglia. Without citing the numerous confirmatory observations of different physiologists, it is sufficient to state that Schiff has experimentally demonstrated, in the most conclusive manner, that the vaso-motor nerves are derived from the cerebro-spinal centres and not from the sympathetic ganglia. There is now no difference of opinion among physiologists upon this point, the only question being the exact location of the vaso-motor centres.

As a summary of our present knowledge of the origin of the vaso-motor nerves in the cerebro-spinal axis, we may cite the following remarks, from a review of the experiments of Schiff, by Brown-Séquard: "1. That if there are vasó-motor elements which decussate in the spinal cord, their number is excessively small. 2. That the facts observed by M. Schiff, on this subject, admit of a more simple explanation. 3. That a number of the vaso-motor elements stop in the spinal cord. 4. That a tolerably large number of vaso-motor elements, coming from different points in the body, ascend as far as the tuber annulare, and some as far as the cerebellum and to other parts of the encephalon. 5. That, consequently, the medulla oblongata is not the sole source of the vaso-motor elements." These statements express pretty much all that we know of the origin of the vaso-motor elements and their decussation, as far as their direct action is concerned; but some important points have been developed by observations upon reflex vaso-motor phenomena, involving a transmission of impressions to the centres through the nerves of general sensibility.

Reflex Phenomena operating through the Sympathetic System.—We shall not discuss, in this connection, the reflex phenomena of secretion, as these have already been considered with sufficient minuteness, nor again treat of reflex action, through the sympathetic, upon the general circulatory system, which has been taken up fully under the head of the depressor-nerve of the circulation, but we shall here describe certain reflex acts, involving vaso-motor phenomena, which we thus far have touched upon very briefly.

As regards animal heat, the phenomena of which are intimately connected with the supply of blood to the parts, we may mention the observations of Brown-Séquard and Lombard, who found that pinching of the skin on one side was attended with a diminution in the temperature in the corresponding member of the opposite side, and that sometimes, when the irritation was applied to the upper extremities, changes were produced in the temperature of the lower limbs. Tholozan and Brown-Séquard found, also, that lowering the temperature of one hand produced a considerable depression in the heat of the other hand, without any notable diminution in the general heat of the body. Brown-Séquard showed that, by immersing one foot in water at 41° Fahr., the temperature of the other foot was diminished about 7° Fahr. in the course of eight minutes. These facts show that certain impressions made upon the sensory nerves affect the animal heat by reflex action. As section of the sympathetic filaments increases the heat in particular parts, with an increase in the supply of blood, and their galvanization reduces the quantity of blood and diminishes the temperature, it is reasonable to infer that the reflex action takes place through the vaso-motor nerves. If we assume that the impression is conveyed to the centres by the nerves of general sensibility, and that the vessels are modified in their caliber and the heat is affected through the sympathetic fibres, we have only to determine the situation of the centres which receive the impression and generate the stimulus. These centres, as we have already seen, are not situated in the sympathetic ganglia, but in the cerebro-spinal axis.

The existence of vaso-motor nerves and their connection with centres in the cerebro-spinal axis are now sufficiently well established. It is certain, also, that centres presiding over particular functions may be distinctly located, as the genito-spinal centre, in the spinal cord opposite the fourth lumbar vertebra, and the cilio-spinal centre, in the cervical region of the cord. A stimulus generated in these centres, sometimes as the result of impressions received through the nerves of general sensibility, produces contraction of the non-striated muscular fibres of the iris, vasa deferentia, etc., including the muscular walls of the blood-vessels. The contraction of the muscular walls of the vessels is tonic; and, when their nerves are divided, relaxation takes place, and the vessels are dilated by the pressure of blood. By this action, the local circulations are regulated in accordance with impressions made upon sensory nerves, the physiological requirements of certain parts, mental emotions, etc. Secretion, the peristaltic movements of the alimentary canal, the movements of the iris, etc., are influenced in this way. This action is also illustrated in cases of reflex paralysis, in inflammations as the result of "taking cold," and in many pathological conditions, of which it is not our province to treat. The facts already noted with regard to the excito-motor action of the spinal cord in the functions of animal life have their analogy in the vaso-motor reflex system. When the centres are destroyed, when the sensory nerves are paralyzed by anæsthetics, or when the true vaso-motor nerves are divided, reflex vaso-motor action is abolished.

The vaso-motor filaments are not confined to the branches of the sympathetic, but they exist as well in the ordinary cerebro-spinal nerves. Bernard has demonstrated this fact in the most conclusive manner. He divided the fourth, fifth, sixth, seventh, and eighth pairs of lumbar nerves on one side in a dog, at the spinal column, and paralyzed motion and sensation in the leg of that side, but the temperature of the two sides remained the same. He afterward exposed and divided the sciatic nerve on that side, and then noted a decided increase of temperature. This experiment, which is only one of a large number, shows conclusively that the ordinary mixed nerves contain vaso-motor fibres, which are entirely independent of the nerves of motion and sensation, a fact which is admitted by all physiologists and has frequently been illustrated in cases of disease in the human subject.

It only remains to show that the phenomena following section of the sympathetic in animals are illustrated in certain cases of disease or injury in the human subject. It is excessively rare to observe traumatic injury confined to the sympathetic in the neck. A single case, however, apparently of this kind, has lately been reported by Mitchell. A man received a gunshot-wound in the neck. Among the phenomena observed a few weeks after, were, contraction of the pupil on the side of the injury, and, after exercise, flushing of the face upon that side. There was no difference in the temperature upon the two sides, during repose, but no thermometric observations were made when half of the face was flushed by exercise. Dr. Bartholow has reported several cases of unilateral sweating of the head (two observed by himself), in several of which there was probably compression of the sympathetic from aneurism. In those cases in which the condition of the eye was observed, the pupil was found contracted in some and dilated in others. In none of these cases were there any accurate thermometric observations. In a series of observations by Wagner, upon the head of a woman, eighteen minutes after decapitation, powerful galvanization of the sympathetic produced great enlargement of the pupil. In such a case as this, it would not be possible to make any observations on the influence of the sympathetic upon the temperature.

Trophic Centres and Nerves (so called).

We have deferred the consideration of the so-called trophic nerves until we had treated of the functions of the sympathetic system, because the vaso-motor nerves, by their influence upon the circulation, are evidently connected with the phenomena of nutrition. It is not necessary to dwell very minutely upon this point; but cases of disease, as well as experiments upon the inferior animals, show that, when a muscle is paralyzed, as a result of the abolition of nervous influence and consequent disease, it becomes atrophied, its fibres lose their characteristic structure and finally become incapable of contracting under a stimulus. As we have seen that the cerebro-spinal nerves, in addition to their motor and sensory fibres, contain vaso-motor elements, it becomes a question whether the muscles be supplied with special nerves—aside from those of motion and sensation and the vaso-motor nerves—which preside over their nutrition. Such could properly be called trophic nerves. Many pathologists, relying upon the presence of certain lesions of cells in the cord, in connection with cases of progressive muscular atrophy, admit the existence of trophic cells and nerves. It must be admitted, however, that these views rest upon pathological facts alone and have not been demonstrated by physiological experiments or observations.

After what we have said, it is evident that proper nutrition of the muscular system depends upon its exercise and the integrity of its motor nerves. In the second place, the history of monsters shows that the muscular system may be developed independently of the cerebro-spinal centres. In the admirable work of Brachet, upon the ganglionic system, numerous cases of anencephalic monsters are detailed, in which the muscular system was found more or less perfectly developed. In some of these, the fœtus was delivered at term and lived for several hours. When we consider the great number of cases of this kind on record, a few of which only are cited by Brachet, it is evident that the cerebro-spinal centres are not absolutely necessary to development *in utero*. Some of the cases reported presented spasmodic movements of certain muscles.

While it is certain that a fœtus may become developed *in utero*, when there is reason to suppose that the cerebro-spinal influence is wanting and the chief nervous operations are effected through the ganglionic system, direct experiments upon the sympathetic in animals do not positively show any influence upon nutrition, except as this system of nerves affects the supply of blood to the parts. When we divide a sympathetic nerve, there is an apparent exaggeration of the nutritive processes in particular parts, and there may be inflammatory phenomena, but atrophy of muscles is not observed. Indeed, we only have atrophy of muscles following division of cerebro-spinal nerves, or, as recently-observed cases of disease have shown, after disorganization of cells belonging to what we recognize as motor centres. As regards the latter condition, there can be no doubt of the fact that progressive muscular atrophy is attended with disorganization of certain of the motor cells of the spinal cord.

Without fully discussing this subject, which belongs to pathology, the facts may be briefly stated as follows: We may have progressive atrophy of certain muscles, which may be uncomplicated with paralysis except in so far as there is weakness of these muscles, due to partial and progressive destruction of their contractile elements. The only pathological condition in these cases, aside from the changes in the muscular tissue, is destruction of certain cells in the antero-lateral portions of the cord, with more or less atrophy of the corresponding anterior roots of the nerves. No one has pretended to have demonstrated cells in the cord, presenting anatomical peculiarities by which they may be distinguished from the ordinary motor or sensory elements, but the fact of the degeneration of certain cells, others remaining normal, and this fact alone, has led to the distinction, by certain writers, of trophic cells; and, of course, these must be connected with the muscles by trophic nerves.

We shall now study the phenomena of progressive muscular atrophy from a physiological point of view, and see if they afford any positive evidence of the existence of special cells and nerves presiding over the nutrition of the muscular system, or whether the phenomena observed cannot be explained by the partial degeneration of the ordinary motor cells and nerves.

There can be no doubt of the fact that the cells of the antero-lateral columns of the spinal cord preside over motion, and that the stimulus generated in these cells is conveyed to the muscles by the anterior roots of the spinal nerves. It is a fact, no less definite, that, when a muscle or a part of a muscle is deprived of the motor stimulus by which it is brought into action, its fibres atrophy, become altered in structure, and lose their contractility. Starting with these two well-defined physiological propositions, and assuming that a few of the ordinary motor cells of the cord are destroyed—we will not call them trophic cells—what are the phenomena to be expected as a consequence of such a lesion? Reasoning from what we know of the physiology of the nervous system, we should expect to find the following conditions:

The destruction of certain motor nerve-cells would certainly produce degeneration of the fibres to which they give origin. This has been observed; for, in this condition, the anterior roots arising from the diseased portions of the cord are atrophied. This occurs when any motor nerves are separated from their cells of origin, and it involves no necessity of assuming the existence of special trophic cells or nerves.

If a few of the motor cells be affected with disease, and if the degeneration be gradual and progressive, we should expect progressive and partial paralysis of the muscles to which their nerves are distributed. This paralysis, confined to a limited number of fibres of particular muscles or sets of muscles, would give the idea of progressive weakening of the muscles, and the phenomena would not be those observed in complete paralysis produced by section of the motor nerves. These are precisely the phenomena observed in progressive muscular atrophy, preceding the paralysis which is the final result of the disease; and these do not involve the action of any special centres or nerves.

As regards the muscular atrophy itself, if the nervous stimulus be progressively destroyed, the muscular tissue will necessarily undergo progressive degeneration and atrophy.

With the above considerations, we leave the trophic cells and nerves to the pathologist; and we can only admit the existence of centres and nerves specially and directly influencing the nutrition of the muscular system, when it has been demonstrated that there are lesions of particular structures in the nervous system, which produce phenomena that cannot be explained by our knowledge of the action of ordinary motor and sensory nerves and of the vaso-motor system.

We have thus endeavored to represent what is actually known concerning the sympathetic system, but it is evident that we have much to learn with regard to its physiology. The great sympathetic ganglia may have functions of which we have no definite idea; and we are better prepared to advance our knowledge in this direction, by admitting our ignorance, than by attempting to supply the deficiencies in our positive information by theories unsupported by facts.

Sleep.

When we remember that about one-third of our existence is passed in sleep, and that, at this time, voluntary motion, sensation, the special senses, and various of the functions of the organism, are greatly modified, the importance of a physiological study of this condition is sufficiently apparent. The subject of sleep is most appropriately considered in connection with the nervous system, for the reason that the most important modifications in function are observed in the cerebro-spinal axis and nerves. Repose is as necessary to the nutrition of the muscular system as proper exercise; but repose of the muscles relieves the fatigue due to exercise, without sleep. It is true that, after violent and prolonged exertion, there is frequently a desire for sleep, but simple repose will often restore the muscular power. After the most violent effort, a renewal of muscular vigor is most easily and completely effected by rest without sleep, a fact familiar to all who are accustomed to athletic exercises. The glands engaged in the production of the true secretions need certain intervals of repose; but this does not necessarily involve sleep. After prolonged and severe mental exertion, however, or after long-continued muscular effort which involves an excessive expenditure of the so-called nerve-force, sleep becomes an imperative necessity. If the nervous system be not abnormally excited by effort, sleep follows moderate exertion as a natural consequence, and it is the only physiological means of complete restoration; but the two most important muscular acts, viz., those concerned in circulation and respiration, are never completely arrested, sleeping or waking, although they undergo certain modifications.

In infancy and youth, when the organism is in process of development, sleep is more important than in adult life or old age. The infant does little but sleep, eat, and digest. In adult life, under perfectly physiological conditions, we require about eight hours of sleep; some persons need less, but very few require more. In old age, unless after extraordinary exertion, less sleep is required than in adult life. Each individual learns by experience how much sleep is necessary for perfect health, and there is nothing which more completely incapacitates one for mental or muscular effort, especially the former, than loss of rest.

Sleeplessness is one of the most important of the predisposing causes of certain forms of brain-disease, a fact which is well recognized by practical physicians. One of the most refined and exquisite methods of torture is long-continued deprivation of sleep; and persons have been known to sleep when subjected to acutely painful impressions. Severe muscular effort, even, may be continued during sleep. In forced marches, regiments have been known to sleep while walking; men have slept soundly in the saddle; persons will sometimes sleep during the din of battle; and other instances illustrating the imperative demand for sleep after prolonged vigilance might be cited. It is remarkable, also, how noises to which we have become accustomed may fail to disturb our natural rest. Those who have been long habituated to the endless noise of a crowded city frequently find difficulty in sleeping in the oppressive stillness of the country. We must have sleep; and this demand is so imperious, that we soon accommodate ourselves to the most unfavorable surrounding conditions. It is remarkable, also, that prolonged exposure to intense cold induces excessive somnolence, and, if this be not resisted, the sleep passes into stupor, the power of resistance to cold becomes rapidly diminished, and death is the inevitable result. Intense heat often produces drowsiness, but, as is well known, is not favorable to natural sleep. We generally sleep less in summer than in winter, though in summer, perhaps, we are less capable of protracted mental and physical exertion.

Sleep is preceded by an indescribable feeling of drowsiness, an indisposition to mental or physical exertion, and a general relaxation of the muscular system. It then requires a decided effort to keep awake; and, if we yield to the soporific tendency, the voluntary muscles cease to act, the lids are closed, we cease to appreciate the ordinary impressions of sound, and we sometimes pass into a dreamless condition, in which we lose all knowledge of existence. We say sometimes, because the mind is not generally inactive during what we may regard as normal sleep. We may have dreams which are not due, as far as can be ascertained, to impressions from the external world received during sleep. Ideas in the form of dreams may be generated in the brain from impressions previously received while awake, or trains of thought may be gradually extended from the moments immediately preceding sleep into the insensible condition.

There may be, during sleep, mental operations of which we have no consciousness or recollection, unconscious cerebration, as it is called by Carpenter. It is well known that we vividly remember dreams immediately on awakening, but that the recollection of them rapidly fades away, unless they be brought to mind by an effort to remember and relate them. Whatever be the condition of the mind in sleep, if the sleep be normal, there is a condition of repose of the cerebro-spinal system and an absence of voluntary effort, which restore the capacity for mental and physical exertion.

The impressionability and the activity of the human mind are so great, most of the animal functions are so subordinate to its influence, and we are so subject to unusual mental conditions, that it is difficult to determine with exactness the phenomena of sleep that are absolutely physiological, and to separate those that are slightly abnormal. We cannot assert, for example, that a dreamless sleep, in which our existence is, as it were, a blank, is the only normal condition of repose of the system; nor can we determine what dreams are due to previous trains of thought, to impressions from the external world received during sleep, and are purely physiological, and what are due to abnormal nervous influence, disordered digestion, etc. We may assume that an entirely refreshing sleep is normal, and that is all.

That reflex ideas originate during sleep, as the result of external impressions, there can be no doubt; and we have already alluded to this point under the head of reflex action. The most remarkable experiments upon the production of dreams of a definite character, by subjecting a person during sleep to peculiar influences, are those of Maury. The hallucinations produced in this way are called hypnagogic, and they occur when the subject is not in a condition favorable to sound sleep. The experiments made by Maury upon himself are so curious and interesting, that we quote the most striking of them in full:

First Observation.—"I was tickled with a feather successively on the lips and inside of the nostrils. I dreamed that I was subjected to a horrible punishment, that a mask of pitch was applied to my face, and then roughly torn off, tearing the skin of the lips, the nose, and the face.

Second Observation.—"A pair of pincers is held at a little distance from my ear, and rubbed with a steel scissors. I dreamed that I heard the ringing of bells; this soon became the tocsin, and I imagined myself in the days of June, 1848.

Third Observation.—"I was caused to inhale Cologne-water. I dream that I am in a perfumer's shop, and the idea of perfumes doubtless awakens the idea of the East: I am in Cairo, in the shop of Jean Farina. Many extravagant adventures follow, the connection of which escapes me.

Fourth Observation.—"I am caused to smell a burning match. I dream that I am at sea (remark that the wind was then blowing in through the windows), and that the Saint-Barbe blew up.

Fifth Observation.—"I am slightly pinched on the nape of the neck. I dream that a blister is applied, which recalls the recollection of a physician who had treated me in my infancy.

Sixth Observation.—"A piece of hot iron is held to my face, keeping it far enough removed, so that the sensation of heat should be slight. I dream of *chauffeurs*, who enter houses and force the inmates, by putting their feet to the fire, to reveal where their money was. The idea of the *chauffeurs* immediately suggests that of the Duchess d'Abrantès, who, I suppose in my dream, has taken me as secretary. I had, indeed, long ago read in the memoirs of this intelligent woman certain details concerning the *chauffeurs*.

Seventh Observation.—"The word *parafagaramus* is pronounced in my ear. I hear nothing, and awake, having had rather a vague dream. The experiment is repeated when I am asleep in my bed, and the word *maman* is pronounced many times in succession. I dream of different things, but in this dream I heard the humming of bees. The same experiment, repeated several days after, when I was scarcely asleep, was more conclusive. The words *Azor*, *Castor*, *Léonore*, were pronounced in my ear; on awaking, I recollected that I had heard the last two words, which I attributed to one of the persons who had conversed with me in my dream.

"Another experiment of the same kind likewise showed that the sound of the word, and not the idea attached to it, had been perceived. The words *chandelle*, *haridelle*, were pronounced in my ear many times in succession. I awoke suddenly of my own accord, saying, *c'est elle.* It was impossible for me to recall what idea I attached to this answer.

Eighth Observation.—"A drop of water is allowed to fall on my forehead. I dream that I am in Italy, that I am very warm, and that I am drinking the wine of Orviette.

Ninth Observation.—"A light, surrounded with a red paper, is many times in succession passed before my eyes. I dream of a tempest of lightning, and all the remembrance of a violent storm which I had encountered in the English Channel, in going from Morlaix to Havre, is present in my mind."

As regards dreams due to external impressions, it is a curious fact, which has been noted by many observers and is one which accords with the personal experience of all who have reflected upon the subject, that trains of thought and imaginary events, which seem to pass over a long period of time in our dreams, actually occur in the brain within a few seconds. A person is awakened by a certain impression, which undoubtedly gives rise to a dream that seems to occupy hours or days, and yet the period of time between the impression and the awakening is hardly more than a few seconds; and persons will drop asleep for a very few minutes, and yet have dreams with the most elaborate details and apparently of great length. It is unnecessary to cite the numerous accounts of literary compositions of merit, the working out of difficult mathematical problems in dreams, etc., some of which are undoubtedly accurate. If it be true, that the mind is capable of forming consecutive ideas during sleep—which can hardly be doubted—there is no good reason why these phenomena should not occur, and the thoughts should not be remembered and noted immediately on awakening. In most dreams, however, the mind is hardly in a normal condition, and the brain generally loses the power of concentration and of accurate reasoning. We sometimes commit atrocious crimes in our dreams, without appreciating their enormity, and we are often placed in the most absurd and impossible conditions, without any idea, at the time, of their extraordinary and unnatural character. This is a fact sufficiently familiar to every one and is one which does not admit of satisfactory explanation.

We have made no attempt to offer an explanation of the curious psychological phenomena presented during sleep, and, indeed, we know little enough of the action of the mind at any time; but we have merely given the above as examples of what we may call reflex mental phenomena. Somnambulism, general anæsthesia, sleep from hypnotics, the so-called magnetic sleep, ecstasy, catalepsy, trance, etc., are abnormal conditions, which we shall only consider in so far as they resemble natural sleep.

Condition of the Brain and Nervous System during Sleep.

As we have already seen, during sleep, the brain may be in a condition of absolute repose—at least, as far as we have any subjective knowledge of mental operations—or we may have more or less connected trains of thought. There is, also, as a rule, absence of voluntary effort, although movements may be made to relieve discomfort from position or external irritation, without awakening. The sensory nerves retain their properties, although the general sensibility is somewhat blunted; and the same may be said of the special senses of hearing, smell, and probably of taste. The peculiar dreams induced in the case of Maury by red lights show that the sense of sight is not entirely lost. There is every reason to believe, however, that the functions of the sympathetic system are not disturbed or affected by sleep, if we except the action of the vaso-motor nerves upon the circulation in the brain.

Two opposite theories have long been in vogue with regard to the immediate cause of sleep. In one, this condition is attributed to venous congestion and increased presssure of blood in the brain, and this view probably had its origin in the fact that cerebral congestion induces stupor or coma. Stupor and coma, however, are entirely distinct from natural sleep; for here, the functions of the brain are suspended, there is no consciousness, no dreaming, and the condition is manifestly abnormal. In animals rendered comatose by opium, the brain may be exposed and is found deeply congested with venous blood. The same condition often obtains in profound anæsthesia from chloroform, but a state of the brain very nearly resembling normal sleep is observed in anæsthesia from ether. These facts have been positively demonstrated by experiments upon living animals, and have been observed in the human subject, in cases of injury of the head. When opium is administered in large doses, the brain is congested during the condition of stupor or coma, but this congestion is relieved when the animal passes, as sometimes happens, from the effects of the agent into a natural sleep. In view of these facts and others which will be stated hereafter, it is unnecessary to discuss the theory that sleep is attended with or is produced by congestion of the cerebral vessels.

The idea that the circulation in the brain is diminished during sleep has long been entertained by certain physiologists; but, until within a few years, it has rested chiefly upon theoretical considerations.

Passing over arguments by the older writers for and against this theory of sleep, we come to the researches of Durham, in 1860, in which it seemed to be demonstrated that the supply of blood to the brain is always greatly diminished during sleep. These experiments were made upon dogs. A piece of the skull, about the size of a shilling, was removed with a trephine, and a watch-glass was accurately fitted to the opening and cemented at the edges with Canada balsam. When the animals operated upon in this way were awake, the vessels of the pia mater were seen moderately distended, and the circulation was active; but, during perfectly natural sleep, the brain retracted and became pale. "The contrast between the appearances of the brain during its period of functional activity and during its state of repose or sleep was most remarkable." There can be hardly any doubt, from these experiments, that the circulation in the cerebral substance is more active when we are awake than during sleep; but the question has been raised by Dr. Cappie, in a very interesting little work upon the causation of sleep, whether, during a state of diminished activity of the capillary circulation in the brain-substance, the veins be not congested, and sleep be immediately due to pressure from these distended vessels on the gray matter. This point is one very difficult to decide, and it has not been made the subject of experimental inquiry. Dr. Cappie accepts, in the main, the experiments of Durham as accurate, but he regards his observations as applying only to the circulation in the arteries and capillaries. His view is that, when the capillary circulation in the brain-substance is diminished in sleep, the nervous matter is more or less collapsed, and that the veins are necessarily congested. At present, however, we can only accept the experimental results of Durham, that the circulation in the brain is notably diminished in sleep.

The influence of diminished supply of blood to the brain has been illustrated by compression of both carotid arteries. In an experiment performed upon his own person, Dr. Fleming produced immediate and profound sleep in this way, and this result invariably followed in subsequent trials upon himself and others. We have, however, the observations of Waller, who produced anæsthesia in patients by pressure upon both pneumogastric nerves; but the nerves are so near the carotid arteries that they could hardly be compressed, in the human subject, without interfering with the current of blood, and such experiments do not positively show whether the loss of sensibility be due to pressure upon the nerves or upon the vessels. In some rare cases, in which both carotid arteries have been ligatured in the human subject, it has been stated that there is an unusual drowsiness following the necessary diminution in the activity of the cerebral circulation; but this result is by no means constant, and the morbid conditions involving so serious an operation are usually such as to interfere with their value as facts bearing upon the question under consideration. As far as the human subject is concerned, the most important facts are the results of compression of both carotids in healthy persons. These, as well as experiments on animals, all go to show that the supply of blood to the brain is very much diminished during natural sleep, and that sleep may be induced by retarding the cerebral circulation by compressing the vessels of supply. When the circulation is interfered with by compressing the veins, congestion is the result, and we have stupor or coma.

If diminished flow of blood through the cerebral vessels be the cause of natural sleep, it becomes important to inquire how this condition of physiological anæmia is brought about. It must be that, when the system requires sleep, the vessels of the brain contract in obedience to a stimulus received through the sympathetic system of nerves, diminishing the supply of blood, here, as in other parts under varied physiological conditions. The vessels of the brain are provided with vaso-motor nerves, and it is sufficient to have noted that the arteries are contracted during sleep, the mechanism of this action being well established by observations upon other parts of the circulatory system. Contraction of the vessels of the pia mater has been observed, although there is some discussion with regard to its exciting cause.

It must be acknowledged that we know but little of the intimate nature of the processes of nutrition of the brain during its functional activity and in repose; but there can be no doubt of the fact that there is more or less cerebral action at all times when we are awake. Although the mental processes are much less active during sleep, even at this time, the operations of the brain are not always suspended. It is equally well established, that exercise of the brain is attended with physiological waste of nervous substance, and, like other parts of the organism, its tissue requires periodic repose to allow of the regeneration of the substance consumed. Analogies to this are to be found in parts that are more easily subjected to direct observation. The muscles require repose after exertion, and the glands, when not actively engaged in discharging their secretions, present intervals of rest. As regards the glands, during the intervals of repose, the supply of blood to their tissue is very much diminished. It is probable, also, that the muscles in action receive more blood than during rest; but it is mainly when these parts are not active, and when the supply of blood is smallest, that the processes of regeneration of tissue seem to be most efficient. As a rule, the functional activity of parts, while it is attended with an increased supply of blood, is a condition more or less opposed to the process of repair, the hyperæmia being, apparently, a necessity for the marked and powerful manifestations of their peculiar functions. When the parts are in active function, the blood seems to be required to keep at the proper standard the so-called irritability of the tissues and to increase their power of action under proper stimulus. Exercise increases the power of regeneration and favors full development, in the repose which follows; but, during rest, the tissues have time to appropriate new matter, and this does not seem to involve a large supply of blood. A muscle is exhausted by prolonged exertion; and the large quantity of blood passing through it carries away carbonic acid, urea, and other products of disassimilation, which are all increased in amount, until it gradually uses up its capacity for work. Then follows repose; the supply of blood is reduced, but, under normal conditions, the tissue repairs the waste which has been excited by action, the blood furnishing nutritive matter and carrying away a comparatively small amount of effete products.

We may safely assume that processes analogous to those just decribed take place in the brain. By absence of voluntary effort, we allow the muscles time for rest and for the repair of physiological waste, and their active function is for the time suspended. As the activity of the brain involves consciousness, volition, the generation of thought, and, in short, the mental condition observed while awake, complete repose of the brain is characterized by the opposite conditions. It is true that we rest the brain without sleep, by abstaining from mental effort, by the gratification of certain of the senses, and by mental distraction of various kinds, and that the mind may work to some degree during sleep; but, during the period of complete repose—that condition which is so necessary to perfect health and full mental vigor—we lose consciousness and volition, there is no thought, and the brain, which does not receive blood enough to stimulate it to action, is simply occupied in the insensible repair of its substance and is preparing itself for future work. The exhaustion of the muscles produces a sense of fatigue of the muscular system, indisposition to muscular exertion, and a desire for rest, not necessarily involving drowsiness. Fatigue of the brain is manifested by indisposition to mental exertion, dulness of the special senses, and a desire for sleep. Simple repose will relieve physiological fatigue of muscles; and, when a particular set of muscles has been used, the fatigue disappears when these muscles alone are at rest, though others be brought into action. Sleep, and sleep alone, relieves fatigue of the brain. When the sleep has continued long enough for the rest of the brain and the repair of its tissue, we awake, prepared for new effort.

We have now only to refer to a new theory of sleep, proposed by Sommer. Taking as a basis the researches of Pettenkofer and Voit upon respiration, Sommer advances the idea that, when the brain is active, or while we are awake, the system appropriates but a small quantity of oxygen in respiration and eliminates a relatively large proportion of carbonic acid; after a time, the oxygen thus appropriated is consumed, and the system demands a new supply; and, during sleep, the organism appropriates oxygen largely and eliminates a relatively small amount of carbonic acid. When the elimination of carbonic acid at the expense of the oxygen stored up reaches a certain point, the necessity for a farther supply of oxygen induces sleep; and when, during sleep, oxygen has been appropriated in sufficient quantity, the system awakes, prepared for a new period of activity of the animal functions.

By reference to the researches of Pettenkofer and Voit, we find that these observers, in experiments upon a man confined in a chamber in which the interchanges of gases in respiration could be estimated, noted, in twenty-four hours, that the subject of the observation, awake but in a condition of complete repose, appropriated sixty-seven per cent. of the entire amount of oxygen of the twenty-four hours during the night, and thirty-three per cent. during the day, while he eliminated fifty-eight per cent. of the entire amount of carbonic acid excreted, during the day, and forty-two per cent., during the night. When the subject of the experiment worked during the day, by turning a heavy wheel, the appropriation of oxygen was thirty-one per cent. for the day, and sixty-nine per cent. for the night; and the elimination of carbonic acid was sixty-nine per cent. for the day, and thirty-one per cent. for the night. According to these observations, the system stores up oxygen at night for use during the day, at this time eliminating a relatively small quantity of carbonic acid; and, during the day, it excretes more carbonic acid than during sleep, appropriating then a relatively small amount of oxygen.

This theory of sleep seems to rest upon observations too restricted to be adopted without reserve. It is stated, indeed, that the first experiments of Pettenkofer and Voit were not confirmed in other observations made upon the same person. It is hardly possible, with our present information, to assume that sleep is due simply to want of oxygen, and it is more in accordance with well-established physiological facts to attribute it to a necessity for the general regeneration of the nervous tissue, though into this, the necessity for oxygen may enter as one element in the physiological repair.

During sleep, nearly all of the functions, except those directly under the control of the sympathetic nervous system, are diminished in activity. The circulation is slower, and the pulsations of the heart are less frequent, as well as the respiratory movements. These points have already been considered under the heads of circulation and respiration. We have but little positive information with regard to the relative activity of the processes of digestion, absorption, and secretion, during sleep. The drowsiness which many persons experience after a full meal is probably due to a determination of blood to the alimentary canal and a consequent diminution in the supply to the brain.

CHAPTER XXIII.

SPECIAL SENSES—TOUCH, OLFACTION, AND GUSTATION.

General characters of the special senses—Muscular sense (so called)—Appreciation of weight—Sense of touch—Variations in tactile sensibility in different parts—Table of variations measured by the æsthesiometer—Connection between the variations in tactile sensibility and the distribution of the tactile corpuscles—Titillation—Appreciation of temperature—Venereal sense—Olfaction—Nasal fossæ—Schneiderian and olfactory membrane—Physiological anatomy of the olfactory nerves—Olfactory bulbs—Olfactory cells and terminations of the olfactory nerve-fibres—Properties and functions of the olfactory nerves—Mechanism of olfaction—Relations of olfaction to the sense of taste—Reflex acts through the olfactory nerves—Gustation—Savory substances—Relations between gustation and olfaction—Taste and flavor—Modifications of the sense of taste—Nerves of taste—Chorda tympani—Facial paralysis with impairment of taste—Paralysis of general sensibility of the tongue without impairment of taste—Glosso-pharyngeal nerve (first division of the eighth)—Physiological anatomy—General properties of the glosso-pharyngeal—Relations of the glosso-pharyngeal nerves to gustation—Mechanism of gustation—Physiological anatomy of the organ of taste—Papillæ of the tongue—Taste-buds, or taste-beakers—Connections of the nerves with the organs of taste.

Our study of the nervous system thus far has involved simply motion and what is known as general sensibility; and almost all our positive knowledge of these properties has been derived from experiments upon the inferior animals. As regards sensation, the experiments have referred to impressions recognized as painful; and we have seen that these are conveyed to the centres by nerve-filaments, anatomically as well as physiologically distinct from those which convey to the contractile parts the stimulus that gives rise to motion. As far as we have studied the sensory nerves, we have alluded to simple impressions only; but it is evident that the filaments of peripheral distribution of these nerves are capable of receiving a variety of impressions, by which we determine, to a certain extent, the form, size, character of surface, density, and temperature of objects. We also have a general appreciation of heat and cold; a sense of resistance, which gives an idea of weight; and, finally, there are nerves of peculiar properties, terminating in organs calculated to receive the impressions of smell, taste, sight, and hearing.

The senses of olfaction, gustation, vision, and audition, belong to peculiar organs, provided with nerves of special properties, which are usually not endowed with general sensibility. These nerves have been omitted in our general study of the nervous system; and the accessory organs to which they are distributed are so important and intricate in their structure as to demand extended description.

The senses of touch, titillation, temperature, and pain are all conveyed to the nerve-centres by what we have described as ordinary sensory nerves; the touch being perfected in certain parts by peculiar arrangements of the terminal nerve-fibres. Although it be possible that each one of these impressions may be transmitted by special and distinct fibres, this has not yet approached a positive demonstration. The so-called muscular sense, by which we appreciate weight, resistance, etc., undoubtedly depends, to a great extent if not entirely, upon the muscular nerves.

Muscular Sense (so called).

It is difficult to define exactly what is meant by the term muscular sense, as it is used by many physiologists. In all probability, the sense which enables us to appreciate the resistance, immobility, and elasticity of substances that are grasped, on which we tread, or which, by their weight, are opposed to the exertion of muscular power, is immensely modified by education and habit. Still, it is undoubtedly true that the general sensibility regulates the action of muscles to a very great extent. If, for example, the lower extremities be paralyzed as regards sensation, the muscular power remaining intact, the person affected cannot walk, unless he be able to see the ground. In these cases, the individual often falls when blindfolded, for the simple reason that his limbs have lost the sense of contact with the ground, which is nothing more nor less than loss of general sensibility. Many curious examples of this kind are to be found in works upon diseases of the nervous system. One of the most striking is a case communicated to Sir Charles Bell by Dr. Ley. The patient was afflicted with partial loss of sensibility upon one side of the body, "without, however, any corresponding diminution of power in the muscles of volition, so that she could hold her child in the arm of that side so long as her attention was directed to it; but, if surrounding objects withdrew her from the notice of the state of her arm, the flexors gradually relaxed, and the child was in hazard of falling." This is something like the phenomena ordinarily described under the head of locomotor ataxia. In this disorder, there is disease of the posterior columns of the spinal cord, with progressive loss of general sensibility, the muscular power, in some instances, being intact. Patients affected in this way are sometimes unable to walk or stand unless they supply the sense of contact by the sight. One of the most characteristic phenomena is inability to stand when blindfolded; although, with the aid of the sight, the muscles can be made by the will to act with great power.

Without entering into a full discussion of the various arguments used for and against the existence of a special "muscular sense," it is sufficient to state that, in those cases in which general sensibility is lost or seriously impaired, the brain has no exact appreciation of the action of the muscles, except as regards the sense of fatigue. This question is of great importance in connection with the pathology of the nervous system; and it seems that the weight of evidence is decidedly in favor of the view that there is no distinct perception of muscular action—aside from general sensibility—that can properly be called a muscular sense.

Habit and education enable us to appreciate with great nicety differences in weight; but this is chiefly due to the sense of resistance to muscular effort and has little dependence upon the sense of touch. In the elaborate and classical experiments of Weber, this point was very strikingly illustrated. The observations of this physiologist upon the sense of touch and general sensibility were very varied and extensive; and, among the most important of the results with regard to the appreciation of pressure and weight, are the following:

In general, those parts which are most sensitive to the impressions of touch, as the fingers, enable us to appreciate differences in pressure and weight with the greatest accuracy. The sense of simple pressure, unaided by the estimation of weight by muscular effort, is generally more acute upon the left side, probably because the integument of the left hand is thinner than that of the right hand. Differences in weight can be accurately distinguished, when they amount to only one-sixteenth, by employing muscular effort in lifting, as well as the sense of pressure; but the sense of pressure alone enables us to appreciate a difference of not less than one-eighth. When weights are tested by lifting with the hand, the appreciation of slight differences is more delicate when the weights are successively tested with the same hand than when two weights are placed, one on either hand. When the interval between the two trials amounts to more than forty seconds, slight differences in weight—the difference between fourteen and a half and fifteen ounces, for example—cannot be accurately appreciated. In such trials, it is necessary to have the metals used of the same temperature, for cold metals seem heavier than warm.

These observations formularized some of the facts, sufficiently evident to every one, relating to the appreciation of slight differences in weight. It is well known that experts acquire, in this regard, wonderful delicacy and accuracy. Those who are in the daily habit of handling coins not only count with astonishing rapidity, but are able to detect and throw out a light piece instantly and with unerring certainty.

Sense of Touch.

We have already considered, in connection with the nervous system, the modes of termination of the sensory nerves; and, in many instances, it is possible to explain, by the anatomical characters of the nerves, the great differences that have been observed in the delicacy of the tactile sensibility in different parts—differences which are exceedingly important, pathologically as well as physiologically, and which have been studied by Weber, Valentin, and others, with great minuteness.

Variations in the Tactile Sensibility in Different Parts.—In certain parts of the cutaneous surface, the general sensibility is much more acute than in others. For example, a sharp blow upon the face is more painful than a similar injury to other parts; and the eye, as is well known, is most exquisitely sensitive. The appreciation of temperature also varies in different parts, this probably depending to a great extent upon habitual exposure. Some parts, as the soles of the feet or the axilla, are peculiarly sensitive to titillation. The sense of touch, however, by which we appreciate the size, form, character of the surface, consistence, etc., of objects, is developed to a greater degree in some parts than in others; a fact which can be very readily explained, in some instances, by the anatomical arrangements of the peripheral sensory nerves. When we wish to ascertain those properties of objects revealed by the sense of touch, we generally employ the fingers. This sense is capable of education and is almost always extraordinarily developed in persons who are deprived of other special senses, as sight or hearing. The blind learn to recognize individuals by feeling of the face. A remarkable instance of this is quoted in works on physiology, of the blind sculptor, Giovanni Gonelli, who was said to model the most striking likenesses entirely by the sense of touch. Other instances of this kind are on record. The blind have been known to become proficients in conchology and botany, guided simply by the sense of touch. It is related of a blind botanist, that he was able to distinguish ordinary plants by the fingers and by the tip of the tongue. It is well known that the blind learn to read with perfect facility, by passing the fingers over raised letters but little larger than the letters in an ordinary folio Bible. Rudolphi cites the remarkable faculty acquired by Baczko, of distinguishing the colors of fabrics by the sense of touch alone.

An exceedingly ingenious and accurate method of determining the relative delicacy of the tactile sensibility of different portions of the cutaneous surface was devised a number of years ago (1829) by E. H. Weber, whose researches upon this subject, which have been repeatedly confirmed by other observers, are still the most careful and reliable on record. This method consists in the application to the skin, of two fine but blunt points, separated from each other by a known distance. The individual experimented upon should be blindfolded, and the points applied to the skin simultaneously. By carefully adjusting the distance between the points, a limit will be reached where the two impressions upon the surface are appreciated as one; *i. e.*, by gradually approximating them, the subject will suddenly feel both points as one, when, an instant before, with the points a little farther removed from each other, he distinctly felt two impressions. This gives a very accurate measure of the delicacy of the tactile as distinguished from the general sensibility of different parts, and it has lately been found a most important guide in the investigation of diseases of the nervous system attended with partial anæsthesia of the surface. Of course, the instrument used may be very simple (a pair of ordinary dividers will answer), but it is convenient to have some ready means of ascertaining the distances between the points. An instrument, consisting simply of a pair of dividers, with a graduated bar giving a measure of the separation of the points, is the best, as it combines simplicity, convenience of use, and portability. This instrument is called the æsthesiometer.

The experiments of Weber were made upon his own person, and, of course, they do not show the variations that may occur in different individuals in health, a point of considerable importance in estimating the extent of anæsthesia in disease. His observations also showed some slight variations with the direction of the line of the two points, but these are not important. Valentin repeated the experiments of Weber, and, in addition, took the maximum, minimum, and mean, in six persons. Aside from these observations, the repetition of Weber's experiments has done little more than confirm the original facts. The table upon the next page, taken from the article on "Touch" by Dr. W. B. Carpenter in the *Cyclopædia of Anatomy and Physiology*, London, 1849–1852, vol. iv., part ii., p. 1169, gives the results obtained by Weber and by Valentin.

If we note the distribution of the tactile corpuscles in connection with this table, it will be seen that the sense of touch is most acute in those situations in which the corpuscles are most abundant. In the space of about one-fiftieth of a square inch on the palmar surface of the third phalanx of the index-finger, Meissner counted the greatest number of corpuscles, viz., one hundred and eight. In this situation, the tactile sensibility is more acute than in any other part of the skin, the mean distance indicated by the æsthesiometer being 0·603 of a line. In the same space on the second phalanx, forty corpuscles were counted, the æsthesiometer marking 1·558 line, this part ranking next in tactile sensibility after the red surface of the lips. We can readily understand how the tactile corpuscles, embedded in the amorphous substance of the cutaneous papillæ, might increase the power of appreciation of delicate impressions by presenting hard surfaces against which the delicate nerve-filaments can be pressed.

As regards those portions of the general cutaneous surface in which no tactile corpuscles have been demonstrated, it is not easy to connect the variations in the tactile sensibility with the nervous distribution, as we know little or nothing of the comparative richness of the terminal nervous filaments in these situations.

Table of Variations in the Tactile Sensibility of Different Portions of the Skin (Weber and Valentin).

The tactile sensibility is measured by the greatest distance between two points at which they convey a single impression when applied simultaneously. The measurements are given in lines ($\frac{1}{12}$ of an inch).

PART OF SURFACE.	WEBER.	VALENTIN.				
		Max.	Min.	Mean.	Relative acuteness.	Relative obtuseness.
Tip of the tongue	0·50	0·50	0·40	0·483	1·000	1·000
Palmar surface of third phalanx of forefinger	1·00	1·00	0·50	0·608	0·802	1·248
do. do. middle finger	....	1·00	0·37	0·706	0·685	1·461
do. do. ring-finger	....	1·00	0·60	0·728	0·669	1·496
do. do. thumb	....	1·00	0·50	0·725	0·667	1·500
do. do. little finger	....	1·00	0·50	0·733	0·659	1·517
Red surface of under lip	2·00	2·00	0·50	1·500	0·322	3·130
do. upper lip	....	2·00	0·50	1·520	0·318	3·145
Palmar surface of second phalanges of fingers	2·00	2·00	1·25	1·558	0·310	3·223
do. first do.	....	1·75	1·50	1·650	0·293	3·414
Middle of the dorsum of the tongue	4·00	4·00	1·50	1·916	0·252	3·964
Dorsal surface of the third phalanges of fingers	3·00	3·00	1·75	2·125	0·227	4·397
Portion of the lips not red	4·00	4·00	1·50	2·208	0·219	4·568
Tip of the nose	3·00	3·00	0·50	2·250	0·215	4·655
Edge of the tongue an inch from the tip	....	4·00	1·50	2·478	0·195	5·127
Lateral surface of the dorsum of the tongue	....	4·00	1·50	2·500	0·193	5·172
Palmar surface of the metacarpus	3·00	3·00	1·75	2·625	0·184	5·431
End of the great-toe	5·00	5·00	3·00	3·250	0·149	6·724
Metacarpal joint of the thumb	4·00	4·50	2·00	3·333	0·145	6·896
External surface of the eyelids	5·00	5·00	2·50	3·833	0·126	7·930
Palm of the hand	5·00	5·00	3·00	3·833	0·126	7·930
Dorsal surface of second phalanx of thumb	5·00	5·50	2·75	3·893	0·124	8·054
do. do. forefinger	....	5·50	2·75	3·893	0·124	8·054
do. do. middle finger	....	5·50	2·75	3·900	0·124	8·069
do. do. little finger	....	5·50	2·50	3·943	0·122	8·158
do. do. ring-finger	....	5·50	2·75	3·971	0·121	8·216
Centre of the hard palate	6·00	6·00	2·00	4·042	0·120	8·363
Mucous membrane of lips close to the gum	9·00	9·00	2·00	4·125	0·117	8·535
Skin of the cheek over buccinator	5·00	5·00	3·25	4·541	0·106	9·395
do. over anterior part of malar bone	7·00	7·00	3·00	4·620	0·105	9·559
Dorsal surface of first phalanges of fingers	7·00	7·00	4·00	4·917	0·098	10·173
Prepuce	....	6·00	4·00	5·100	0·095	10·552
Dorsal surface of heads of metacarpal bones	8·00	8·00	3·25	5·250	0·092	10·862
Skin of cheek over posterior part of malar bone	10·00	10·00	3·00	5·286	0·091	10·936
Plantar surface of metacarpal bone of great-toe	....	7·00	5·00	5·875	0·082	12·155
Lower part of forehead	10·00	10·00	4·00	6·000	0·081	12·414
Back of the hand	14·00	14·00	3·50	6·966	0·069	14·412
Lower part of hairy scalp in occipital region	12·00	12·00	6·00	8·292	0·058	17·156
Surface of the throat beneath lower jaw	15·00	15·00	3·00	8·292	0·058	17·156
Back of the heel	10·00	10·00	8·00	9·000	0·054	18·621
Pubes	....	14·00	3·00	9·200	0·052	19·035
Crown of the head	15·00	15·00	5·50	9·583	0·050	19·827
Patella and surrounding part of thigh	16·00	16·00	6·00	10·208	0·047	21·120
Areola around nipple	....	20·00	9·50	12·066	0·040	24·964
Dorsum of foot near the toes	18·00	18·00	7·50	12·525	0·039	25·914
Axilla	....	14·00	12·00	13·000	0·037	26·897
Upper and lower extremities of forearm	18·00	18·00	7·00	13·292	0·036	27·501
Back of the neck near the occiput	24·00	24·00	8·00	13·292	0·036	27·501
Upper and lower extremities of leg	18·00	18·00	9·00	13·708	0·035	28·361
Penis	18·00	18·00	10·00	13·850	0·034	28·655
Acromion and upper part of arm	18·00	18·00	6·00	13·886	0·034	28·688
Sacral region	18·00	18·00	7·50	14·958	0·032	30·948
Sternum	20·00	20·00	8·00	15·875	0·030	32·845
Gluteal region and neighboring part of thigh	18·00	18·00	10·50	16·625	0·029	34·397
Middle of forearm where its circumference is greatest	30·00	30·00	8·75	17·083	0·028	35·344
Middle of thigh do.	30·00	30·00	9·00	17·633	0·027	36·482
Middle of cervical vertebræ	30·00	30·00	7·00	18·542	0·026	38·362
Five upper dorsal vertebræ	24·00	24·00	11·00	19·000	0·025	39·310
Lower part of thorax and over lumbar vertebræ	•24·00	24·00	11·50	19·912	0·022	44·758
Middle of dorsal vertebræ	30·00	30·00	11·00	24·208	0·020	50·086

Titillation.—The sensation experienced when certain parts of the general surface are subjected to titillation cannot easily be described, although it is sufficiently familiar. This sensation is due simply to delicate impressions made in unusual situations and is remarkable chiefly on account of the reflex movements which it occasions. If the soles of the feet be tickled, it is almost impossible to avoid movements of the limbs. These are not due entirely to the peculiar sensation appreciated by the brain, for the same stimulus, in persons suffering from complete paralysis of sensation and voluntary motion of the lower extremities, may produce even violent action of the paralyzed muscles. The peculiar

48

nature of the sensation is due to the unusual character of the impression, and it does not involve the action of special nerve-fibres as conductors.

Appreciation of Temperature.—It is not known that the sense of temperature, either of the surrounding medium or of bodies applied to different parts of the skin, is appreciated through any nerves other than those of general sensibility, or that there is any special arrangement of the terminations of certain of the nerves connected with this sense. As regards the general temperature, the sense is relative and is much modified by habit. This statement needs no explanation. As is well known, what is cold for an inhabitant of the torrid zone would be warm for one accustomed to an excessively cold climate. Habitual exposure also modifies the sense of temperature. Many persons not in the habit of dressing warmly suffer but little in extremely cold weather. Those who habitually expose the hands, or even the feet, to cold, render these parts quite insensible to temperature; and the same is true of those who often expose the hands, face, etc., to heat.

The variations in the sensibility of different parts of the surface to temperature depend, as we have just indicated, to a great extent upon habit, exposure, etc., but also upon special properties of the parts themselves. The differences, however, are not so marked as to be of any great importance, and the experiments made upon this point are simply curious. It is remarkable, however, to note the exquisite sensibility to variations in temperature sometimes presented by those who are deprived of other senses. The example is quoted by Dunglison, of Dr. Saunderson, formerly Professor of Mathematics at Cambridge, England, who, "when some of his pupils were engaged in taking the altitude of the sun, could tell, by the slight modification in the temperature of the air, when very light clouds were passing over the sun's disk."

The experiments of Weber show conclusively that the skin is the main organ for the appreciation of temperature, if we except the mouth, palate, vagina, and rectum, by which the difference between warm and cold substances is readily distinguished. In several instances in which large portions of the skin were destroyed by burns and other injuries, experiments have been made by applying spatulas of different temperatures. At one time a spatula plunged in water at from 48° to 55° Fahr. was applied to a denuded surface, and again, a spatula at from 113° to 122° Fahr. When the patient was requested to tell which was the warmer, the answers were as frequently incorrect as they were correct; but the discrimination was easy and certain when the applications were made to the surrounding healthy skin. When applications at a higher temperature were made to the denuded part, the patient suffered only pain.

The venereal sense, which we shall not attempt to describe, is unlike any other sensation, and is general, as well as referable to the organs of generation. In this connection, however, it is interesting to note that the tactile sensibility of the palmar surface of the third phalanx of the fingers, measured by the æsthesiometer, compared with the sensibility of the penis, is as 0·802 to 0·034, or between twenty-three and twenty-four times greater.

Olfactory Nerves.

The nerves directly connected with the senses of olfaction, vision, and audition, are but slightly if at all endowed with general sensibility. As regards the olfactory nerves, the parts to which they are distributed are so fully supplied with branches from the fifth, that it is difficult to determine the fact of their sensibility or insensibility to ordinary impressions. The olfactory nerves, however, are distributed to the mucous membrane of that portion of the nasal cavity endowed with the special sense of smell. Before taking up their physiological anatomy, we shall describe briefly the parts to which the olfactory sense is probably confined.

Nasal Fossæ.—The two irregularly-shaped cavities in the middle of the face, opening in front by the anterior nares and connected with the pharynx by the posterior nares, are called the nasal fossæ. The membrane lining these cavities is generally called the Schneiderian mucous membrane, and sometimes, particularly by the French, the pituitary membrane. This membrane is closely adherent to the fibrous coverings of the bones and cartilages by which the nasal fossæ are bounded, and it is thickest over the turbinated bones. It is continuous with the membrane lining the pharynx, the nasal duct and lachrymal canals, the Eustachian tube, the frontal, ethmoidal, and sphenoidal sinuses, and the antrum. There are openings leading from the nasal fossæ to all of these cavities.

The essential organ of olfaction is the mucous membrane lining the upper half of the nasal fossæ. Not only has it been shown anatomically that this part only of the membrane receives the terminal filaments of the olfactory nerves, but physiological experiments have demonstrated that it is the only part capable of receiving odorous impressions. If a tube be introduced into the nostril, placed horizontally over an odorous substance so that the emanations cannot penetrate its caliber, no odor is perceived, though the parts below the end of the tube might receive the emanations; but, if the tube be now directed toward the odorous substance, so that the emanations can penetrate to the upper portion of the nares, the odor is immediately appreciated.

That portion of the lining of the nasal fossæ properly called the olfactory membrane extends from the cribriform plate of the ethmoid bone downward a little less than an inch. It is exceedingly soft and friable, very vascular, thicker than the rest of the Schneiderian membrane, and, in man, has rather a yellowish color. It is covered by long, delicate, columnar cells, nucleated, each one provided with from three to eight ciliary processes, their movement being from before backward. The mucous glands of the olfactory membrane are numerous, long, and racemose. They secrete a fluid which keeps the surface moist, a condition essential to the accurate perception of odorous impressions.

Physiological Anatomy of the Olfactory Nerves.—The apparent origin of the olfactory nerve is by three roots, from the inferior and internal portion of the anterior lobe of the

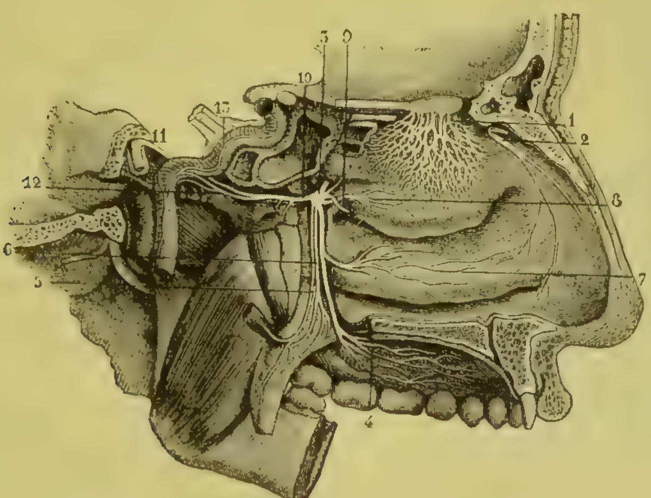


FIG. 288.—*Olfactory ganglion and nerves.* (Hirschfeld.)

1, *olfactory ganglion and nerves*; 2, branch of the nasal nerve; 3, spheno-palatine ganglion; 4, 7, branches of the great palatine nerve; 5, posterior palatine nerve; 6, middle palatine nerve; 8, 9, branches from the spheno-palatine ganglion; 10, 11, 12, Vidian nerve and its branches; 13, external carotid branch from the superior cervical ganglion.

cerebrum, in front of the anterior perforated space. The three roots are an external and an internal white root, and a middle root composed of gray matter. The external white root is long and delicate, passing outward across the fissure of Sylvius to the middle lobe of the cerebrum. The internal white root is thicker and shorter than the external root, and it arises from the most posterior portion of the anterior lobe. The middle, or gray root arises from a little eminence of gray matter situated on the posterior and inner portion of the inferior surface of the anterior lobe.

The deep origin of these three roots of the olfactory nerves is still a matter of discussion. The external root is stated by various anatomists to originate from the corpus striatum, the optic thalamus, the anterior commissure, and the island of Reil; but researches upon this point have been by no means satisfactory. The same uncertainty exists with regard to the deep origin of the internal white root and the gray root.

The three roots of the olfactory converge to form a single nervous cord at the inner boundary of the fissure of Sylvius. This passes forward and slightly inward in a deep groove between two convolutions on the under surface of the anterior lobe, covered by the arachnoid membrane, to the ethmoid bone. This portion of the nerve is exceedingly soft and friable. It is composed of both white and gray matter, the proportions being about two-thirds of the former to one-third of the latter. The gray substance, derived from the gray root, is situated at the upper portion of the nerve, the white substance occupying the inferior and the lateral portions.

By the side of the crista galli of the ethmoid bone, the nerve-trunk expands into an oblong ganglion, called the olfactory bulb. This is grayish in color, excessively soft, and contains the ordinary ganglionic elements. From the olfactory bulb, from fifteen to eighteen nervous filaments are given off, which pass through the foramina in the cribriform plate of the ethmoid bone. These filaments are composed entirely of nerve-fibres and are quite resisting, owing to fibrous elements prolonged from the dura mater. It is strictly proper, perhaps, to regard these as the true olfactory nerves, the cord leading from the olfactory bulb to the cerebrum being more properly a commissure. Having passed through the cribriform plate, the olfactory nerves are distributed to the olfactory membrane in three groups: an inner group, distributed to the mucous membrane of the upper third of the septum; a middle group, to the upper portion of the nasal fossæ; and an outer group, to the mucous membrane covering the superior and middle turbinated bones and a portion of the ethmoid.

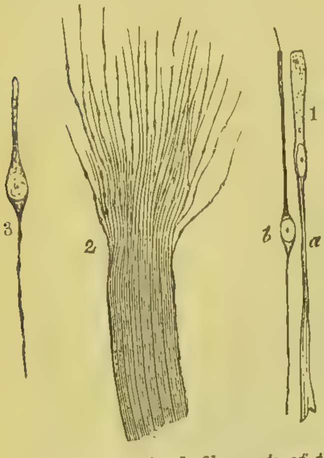


FIG. 234.—*Terminal filaments of the olfactory nerves; magnified* 30 *diameters.* (Kölliker.)

1, from the frog.—*a*, epithelial cells of the olfactory region; *b*, olfactory cells. 2, small branch of the olfactory nerve of the frog, separating at one end into a brush of varicose fibrils. 3, olfactory cell of the sheep.

The mode of termination of the olfactory nerves differs from that of the ordinary sensory nerves, and is peculiar and characteristic, as it is in the other organs of special sense. According to recent observations, the olfactory mucous membrane contains peculiar terminal nerve-cells, called the olfactory cells, which are situated between the cells of epithelium. These are long, delicate, spindle-shaped structures, varicose, each one containing a clear, round nucleus. The appearance of these, which are considered as the true olfactory organs, is represented in Fig. 234. In the frog, there is a fine, hair-like process projecting from each cell beyond the mucous membrane, which has not been observed in man or the mammalia. The great delicacy of the structures entering into the composition of the olfactory membrane renders the investigation of the termination of its nervous filaments exceedingly difficult.

Properties and Functions of the Olfactory Nerves.—It is almost certain that the olfactory nerves possess none of the general properties of the ordinary nerves belonging to the cerebro-spinal system, but that they are endowed with the special sense of smell alone. As far as we know, no one has exposed and operated upon the filaments coming from the olfactory bulbs and distributed to the pituitary membrane in living animals; but experiments upon the nerves behind the olfactory bulbs show that they are entirely insensible to ordinary impressions. Attempts have been made to demonstrate, in the human subject, the special properties of these nerves, by passing a galvanic current through the nostrils; but the situation of the nerves is such that these observations are of necessity indefinite and unsatisfactory. On one or two occasions, in witnessing surgical operations upon the upper part of the nasal fossæ, we have been struck with the exceedingly dull sensibility of its mucous membrane.

The question as to whether or not the olfactory nerves endow the membrane of the nasal fossæ with the sense of smell hardly demands discussion at the present day. It must be evident to any one who reads the experiments of Magendie, in which he attempted to show that the sense of smell was retained after division of these nerves, that he confused the general sensibility of the parts with the peculiar impressions of odors; and the cases, especially the one reported by Bernard, in the human subject, in which it was supposed that the olfactory sense existed notwithstanding congenital absence of the olfactory nerves and bulbs, are by no means satisfactory, in view of the numerous instances in which precisely the opposite has been observed.

Among the numerous experiments upon the higher orders of animals, in which the olfactory nerves have been divided, we may cite, as open to no objections, those of Vulpian and Philipaux, upon dogs. It is well known that the sense of smell is usually very acute in these animals. Upon dividing or extirpating the olfactory bulbs, "after the animal had completely recovered, it was deprived of food for thirty-six or forty-eight hours; then, in its absence, a piece of cooked meat was concealed in a corner of the laboratory. Animals, successfully operated upon, then taken into the laboratory, never found the bait; and nevertheless, care had been taken to select hunting-dogs." This experiment is absolutely conclusive; more so than those in which animals deprived of the olfactory bulbs were shown to eat fæces without disgust, for this sometimes occurs in dogs that have not been mutilated.

Comparative anatomy shows that the olfactory bulbs are generally developed in proportion to the acuteness of the sense of smell. Pathological facts also show, in the human subject, that impairment or loss of the olfactory sense is coincident with injury or destruction of these ganglia. Numerous cases have been reported in which the sense of smell was lost or impaired from injury to the olfactory nerves. In nearly all of the cases on record, the general sensibility of the nostrils was not affected. In 1864, we had an opportunity of examining the following very remarkable case of gunshot wound of the head, in which, among other injuries, the sense of smell was destroyed:

The patient was a soldier, twenty-three years of age, who was shot through the head with a rifle-ball, May 3, 1863. The ball entered on the left side, $1\frac{1}{4}$ inch behind and $\frac{3}{4}$ of an inch below the outer canthus of the eye, emerging at nearly the corresponding point on the opposite side. Small pieces of bone were discharged from time to time for three months from openings in the posterior nares and the throat. He was examined May 10, 1864, when the wounds had healed with falling in of the face over the left malar and nasal bones. He had then entirely lost the power of distinguishing odors. Upon applying acetic acid to the nostrils, he stated that he felt a prickling sensation, but no odor. Dilute ammonia produced a warm sensation. Chloroform gave no sensation. He had no sensation from the emanations of flowers. There was loss of general sensibility of the nasal mucous membrane on the left side, with diminished sensibility on the right side. He had a sensation, not very definite, when in water-closets, where (as he was told) the odor was very offensive, but he experienced no sensation unless the emanations were very powerful. Before entering the army, he was a photographer by trade and was familiar with the odors of acetic acid and ammonia. In this case, it is almost certain that the olfactory nerves had been divided, although other injuries undoubtedly existed.

Mechanism of Olfaction.

There can be no doubt at the present day with regard to the mechanism of the sense of smell. Substances endowed with odorous properties give off material emanations, which must come in contact with the olfactory membrane before their peculiar odor is appreciated. As we have seen, this membrane is situated high up in the nostrils, is peculiarly soft, is provided with numerous glands, by the secretions of which its surface is kept in proper condition, and it possesses the peculiar nerve-terminations of the olfactory filaments.

In experimenting upon the sense of smell, it has been found quite difficult to draw the exact line of distinction between impressions of general sensibility and those which attack the special sense, or, in other words, between irritating and odorous emanations; and the vapors of ammonia, acetic acid, nitric acid, etc., undoubtedly possess irritating properties which greatly overshadow their odorous qualities. It is unnecessary, in this connection, to discuss the different varieties of odors recognized by some of the earlier writers, as the fragrant, aromatic, fetid, nauseous, etc., distinctions sufficiently evident from their mere enumeration; and it is plain enough that there are emanations, like those from delicately-scented flowers, which are easily recognizable by the sense of smell while they make no impression upon the ordinary sensory nerves. The very marked individual differences in the delicacy of the olfactory organs in the human subject and in different animals is an evidence of this fact. Hunting-dogs recognize odors to which we are absolutely insensible; and certain races of men are said to possess a wonderful delicacy of the sense of smell. Like all of the other special senses, olfaction may be cultivated by attention and practice, as is exemplified in the delicate discrimination of wines, qualities of drugs, etc., by experts.

After what we have said concerning the situation of the true olfactory membrane in the upper part of the nasal fossæ and the necessity of particles impinging upon this membrane in order that their odorous properties may be appreciated, it is almost unnecessary to state that the passage of odorous emanations to this membrane by inspiring through the nostrils is essential to olfaction, so that animals or men, after division of the trachea, being unable to pass the air through the nostrils, are deprived of the sense of smell. The act of inhalation through the nose, when we wish to appreciate a particular odor, is an illustration of the mechanism by which the odorous particles may be brought at will in contact with the olfactory membrane.

It is a curious point to determine whether the sense of smell be affected by odors passing from within outward through the nasal fossæ. Persons who have offensive emanations from the respiratory organs usually are not aware, from their own sensations, of any disagreeable odor. This fact is explained by Longet on the supposition that the olfactory membrane becomes gradually accustomed to the odorous impression, and therefore it is not appreciated. This is an apparently satisfactory explanation, for we could hardly suppose that the direction of the emanations, provided they came in contact with the membrane, could modify their effects. He cites a case of cancer of the stomach, in which the vomited matters were exceedingly fetid. At first, the patient, when he expired the gases from the stomach through the nostrils, perceived a disagreeable odor at each expiration; but little by little this impression disappeared.

Relations of Olfaction to the Sense of Taste.—The relations of the sense of smell to gustation are very intimate. In the appreciation of delicate shades of flavor, it is well known that the sense of olfaction plays so important a part, that it can hardly be separated from gustation. The common practice of holding the nose when disagreeable remedies are swallowed is another illustration of the connection between the two senses. In most cases of anosmia, there is inability to distinguish delicate flavors; and patients can distinguish by the taste only sweet, saline, acid, and bitter impressions.

It is undoubtedly true that we lose the delicacy of the sense of taste when the sense of smell is abolished. The experiment of tasting wines blindfolded and with the nostrils plugged, and the partial loss of taste during a severe coryza, are sufficiently familiar illustrations of this fact. In the great majority of cases, when there is complete anosmia, the taste is sensibly impaired; and, in cases in which this does not occur, it is probable that the savory emanations pass from the mouth to the posterior portion of the nasal fossæ, and that here the mucous membrane is not entirely insensible to special impressions.

It is unnecessary, in this connection, to describe fully the reflex phenomena which follow impressions made upon the olfactory membrane. The odor of certain sapid substances, under favorable conditions, will produce an abundant secretion of saliva and even of gastric juice, as has been shown by experiments upon animals. Other examples of the effects of odorous impressions of various kinds are sufficiently familiar.

Gustation.

The special sense of taste enables us to appreciate what is known as the savor of certain substances introduced into the mouth; and this sense exists, in general terms, in parts supplied by filaments from the lingual branch of the fifth and the glosso-pharyngeal nerves.

It is somewhat difficult to define precisely what is meant by savory substances. The word savory is frequently used so as to include the quality of odor; and, indeed, the senses of gustation and olfaction are quite closely connected. Almost all substances that affect the sense of taste possess a certain odor, and taste and smell are thus simultaneously impressed. Medicinal articles of a disagreeable taste may sometimes be swallowed without making a very disagreeable impression, if the nares be closed. Again, when the nares are closed or when the sense of smell is rendered obtuse by an affection of the Schneiderian membrane, it is difficult to distinguish delicate shades of flavor, as the differences in wines. This is a matter of common observation and remark. There are, also, certain articles which have a repulsive odor, the taste of which is not disagreeable, such as some varieties of old cheese. As a rule, however, articles agreeable to the taste possess an agreeable odor, and the senses of taste and smell are not easily separated from each other. These facts have led to a distinction—which cannot, however, be always made with accuracy—between true tastes and flavors. It is assumed by some physiologists, that the true tastes are quite simple, presenting the qualities which we recognize as sweet, acid, saline, and bitter; while the more delicate shades of what are called flavors nearly always involve olfactory impressions, which it is difficult to separate entirely from gustation.

If we apply the term savor exclusively to the quality which makes an impression upon the sense of taste, we recognize that the sensation is special in its character and different from the tactile sensibility of the parts involved and from the sensation of temperature. The terminal filaments of the gustatory nerves are impressed by the actual contact of savory substances, which must, of necessity, be soluble. To a certain extent, there is a natural classification of savors, some of which are agreeable, and others disagreeable; but even this distinction is modified by habit, education, and various other circumstances. Articles that are unpleasant in early life often become agreeable in later years. Inasmuch as the taste is, to some extent, an expression of the nutritive demands of the system, it is found to vary under different conditions. Chlorotic females, for example, frequently crave the most unnatural articles, and these morbid tastes may disappear under appropriate treatment. Inhabitants of the frigid zones seem to crave fatty articles and will even drink rancid oils with avidity. Patients often become accustomed to the most disagreeable remedies and take them without repugnance. Again, the most savory dishes may even excite disgust, when the sense of taste has become cloyed, while abstinence sometimes lends a delicious flavor to the simplest articles of food. The taste for certain articles is certainly acquired, and this is almost always true of tobacco, now so largely used in civilized countries.

Any thing more than the simplest classification of savors is difficult, if not impossible. We recognize that certain articles are bitter or sweet, empyreumatic or insipid, acid or alkaline, etc., but, beyond these simple distinctions, the shades of difference are closely connected with olfaction and are too delicate and numerous for detailed description. Many persons are comparatively insensible to nice distinctions of taste, while others recognize with facility the most delicate differences. Strong impressions may remove, for a time, the appreciation of less powerful and decided flavors. The tempting of the appetite by a proper gradation of gustatory and odorous impressions is illustrated in the modern *cuisine*, which aims at an artistic combination and succession of dishes and wines, so that the agreeable sensations are prolonged to the utmost limit. This may often be regarded as a violation of strictly hygienic principles, but it none the less exemplifies the cultivation of the sense of taste.

In discussing the physiology of taste, we shall avoid an elaborate and artificial classification of savory articles, and shall use the terms sweet, acid, bitter, etc., as they are commonly understood. We shall first describe the physiological anatomy and properties of the gustatory nerves, and then consider the mechanism of gustation, the special organs of taste, and the probable mode of connection between the organs of taste and the nerves.

Nerves of Taste.—Two nerves, the chorda tympani and the glosso-pharyngeal, preside over the sense of taste. These nerves seem to be distributed to distinct portions of the gustatory apparatus and to have somewhat different functions. The chorda tympani has already been referred to as one of the branches of the facial; the glosso-pharyngeal, one of the nerves of the eighth pair, has not yet been described.

Chorda Tympani.—In the description we have given of the facial, the chorda tympani is spoken of as the fourth branch. It passes through the tympanum, between the ossicles of the ear, and joins the inferior maxillary division of the fifth, at an acute angle, between the two pterygoid muscles, becoming so closely united with it that it cannot be followed farther by ordinary dissection. (See Fig. 202, p. 622.) It is impossible to determine with certainty from what root the filaments of this branch derive their origin, whether from the main trunk or the intermediary nerve of Wrisberg; but experiments have shown that it possesses functions entirely distinct from those of the other branches of the facial. The lingual branch of the inferior maxillary division of the fifth has been called the gustatory branch; but this is an error; for, as we shall see, the fifth has nothing to do with gustation, except that it is joined with filaments of the chorda tympani, which reach the tongue through the lingual branch.

As regards the course of the filaments of the chorda tympani after this nerve has joined the fifth, there can be no doubt, both from the effect upon taste and the alteration of the nerve-fibres following its division. Vulpian and Prevost, by the so-called Wallerian method, after dividing the chorda tympani, found degenerated fibres at the terminations of the lingual branch of the fifth in the mucous membrane of the tongue, the fibres being examined ten days or more after the section. It is well known that, a number of days after the section of a nerve, its fibres of distribution undergo change, and these observations leave no doubt of the fact that the chorda tympani is really distributed to the lingual mucous membrane. Observations upon the sense of taste show that the chorda tympani is distributed to about the anterior two-thirds of the tongue.

The general properties of the chorda tympani have only been ascertained by observations made after its paralysis or division. All experiments in which excitation has been applied directly to the nerve in living animals have been negative in their results. Longet states that, when the nerve has been isolated as completely as possible and all reflex action is excluded, its galvanization produces no movement in the tongue.

It is now established beyond question that, in cases of facial palsy in which the lesion affects the root so deeply as to involve the chorda tympani, there is loss of taste in the anterior two-thirds of the tongue, tactile sensibility being unaffected; and numerous cases illustrating this fact have been cited by various authors. Aside from cases of paralysis of the facial with impairment of taste, in which the general sensibility of the tongue is intact, numerous instances are on record of affections of the fifth pair, in which the tongue is absolutely insensible to ordinary impressions, the sense of taste being preserved. A number of such cases have been reported, which show conclusively that the fifth pair presides over general sensibility only, and that it is not a gustatory nerve, except by virtue of filaments derived from the chorda tympani.

Passing from the consideration of pathological cases to experiments upon living animals, the results are equally satisfactory. Although it is somewhat difficult to observe impairment of taste in animals, Bernard and others have succeeded in training dogs and cats so as to observe the effects of colocynth and various sapid substances applied to the tongue. In a great number of experiments of this kind, it has been observed that, after section of the chorda tympani or of the facial so as to involve the chorda tympani, the sense of taste is abolished in the anterior two-thirds of the tongue on the side of the section. However this result may be explained, the fact remains, that section of the nerve in the lower animals is followed by the same results as those observed in pathological observations. In a remarkable case reported by Moos, the introduction of an artificial membrana tympani was followed by loss of taste upon the corresponding side of the tongue, and upon both sides, when a membrane was introduced into each ear. This disappeared when the membranes were removed, and the phenomena were referred to pressure upon the chorda tympani. Experimenters are somewhat at variance with regard to the effects observed upon animals, some asserting that the sensations of taste are simply delayed in their manifestation; but we must remember the difficulty of such observations, and we are to rely mainly upon the unmistakable phenomena noted in cases of affection of the chorda tympani in the human subject.

It seems tolerably certain, first, that the gustatory filaments of the lingual branch of the fifth are derived exclusively from the chorda tympani; second, that the chorda tympani, viewed as a gustatory nerve, is really a branch of the facial; third, that many cases of paralysis of the entire large root of the fifth, in the human subject, present loss of general sensibility in the tongue and no alteration of taste; and fourth, that paralysis of the facial, behind the origin of the chorda tympani, is attended with loss of taste in the anterior two-thirds of the tongue, without any affection of the general sensibility of this organ.

As a summary of our knowledge regarding the gustatory properties of the anterior two-thirds of the tongue, certainly in the human subject, it may be stated without reserve, that these properties depend upon the chorda tympani, its gustatory filaments being derived from the facial and taking their course to the tongue with the lingual branch of the inferior maxillary division of the fifth. In addition, the lingual branch of the fifth contains filaments, derived from the large root of this nerve, which endow the mucous membrane with general sensibility.

Glosso-Pharyngeal Nerve (*First Division of the Eighth*).—The glosso-pharyngeal is distributed to those portions of the gustatory mucous membrane not supplied by filaments from the chorda tympani. It is undoubtedly a nerve of taste; and the question of its other functions will be fully considered in connection with its general properties, as well as the differences between this nerve and the chorda tympani. We have mentioned this nerve in another chapter as the first division of the eighth pair according to the classification of Willis, but we have to treat of its physiological anatomy in this connection, as its most important function is in connection with gustation.

Physiological Anatomy of the Glosso-Pharyngeal.—The apparent origin of the glosso-pharyngeal is from the groove between the lateral tracts of the medulla oblongata and the inferior peduncle of the cerebellum, between the roots of the auditory nerve above and the pneumogastric below. A number of its filaments of origin come from the medulla and a portion from the peduncle. The deep origin is nearly the same as that of the pneumogastric, its filaments arising primarily from the gray substance of the medulla oblongata. From this origin, the filaments pass forward and outward to the posterior foramen lacerum, which the nerve enters in company with the pneumogastric, the spinal accessory, and the internal jugular vein. At the upper portion of the foramen, is a small ganglion, the jugular ganglion, including only a portion of the root. Within the foramen, is the main ganglion, including all of the filaments of the trunk, called the petrous ganglion, or the ganglion of Andersch, after the anatomist by whom it was first described.

At or near the ganglion of Andersch, the glosso-pharyngeal usually receives a delicate filament from the pneumogastric. This communication is sometimes wanting. The same may be said of a small filament passing to the glosso-pharyngeal from the facial, which is not constant. Branches from the glosso-pharyngeal go to the otic ganglion and to the carotid plexus of the sympathetic.

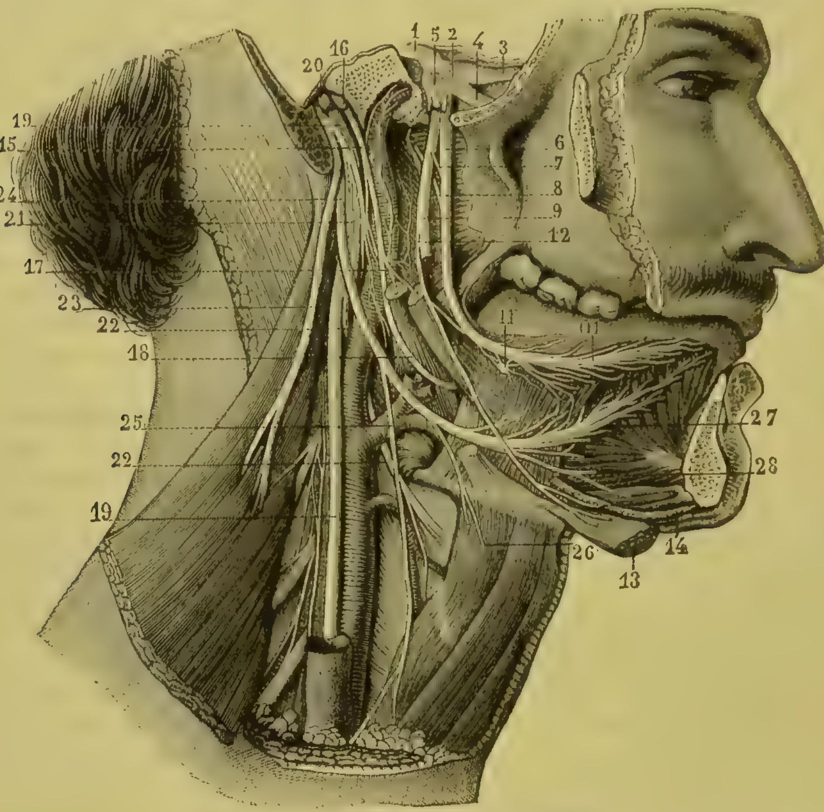


FIG. 285.—*Glosso-pharyngeal nerve.* (Sappey.)

1, large root of the fifth nerve; 2, ganglion of Gasser; 3, ophthalmic division of the fifth; 4, superior maxillary division; 5, inferior maxillary division; 6, 10, *lingual branch of the fifth, containing the filaments of the chorda tympani*; 7, branch from the sublingual to the lingual branch of the fifth; 8, *chorda tympani*; 9, inferior dental nerve; 11, submaxillary ganglion; 12, mylo-hyoid branch of the inferior dental nerve; 13, anterior belly of the digastric muscle; 14, section of the mylo-hyoid muscle; 15, 18, *glosso-pharyngeal nerve*; 16, *ganglion of Andersch*; 17, *branches from the glosso-pharyngeal to the stylo-glossus and the stylo-pharyngeus muscles*; 19, 19, pneumogastric; 20, 21, ganglia of the pneumogastric; 22, 22, superior laryngeal nerve; 23, spinal accessory; 24, 25, 26, 27, 28, sublingual nerve and branches.

The distribution of the glosso-pharyngeal is quite extensive. The tympanic branch, the nerve of Jacobson, arises from the anterior and external part of the ganglion of Andersch, and enters the cavity of the tympanum, where it divides into six branches. Of these six branches, two posterior are distributed to the mucous membrane of the fenestra rotunda and the membrane surrounding the fenestra ovalis; two anterior are distributed, one to the carotid canal, where it anastomoses with a branch from the superior cervical ganglion, and the other to the mucous membrane of the Eustachian tube; two superior branches are distributed to the otic ganglion and, as is stated by some anatomists, to the spheno-palatine ganglion.

A little below the posterior foramen lacerum, the glosso-pharyngeal sends branches to the posterior belly of the digastric and to the stylo-hyoid muscle. There is also a branch which joins a filament from the facial to the stylo-glossus.

Opposite the middle constrictor of the pharynx, three or four branches join branches from the pneumogastric and the sympathetic to form together the pharyngeal plexus. This plexus contains numerous ganglionic points, and filaments of distribution from the three nerves go to the mucous membrane and to the constrictors of the pharynx. Probably, the mucous membrane is supplied by the glosso-pharyngeal. As we have stated in another chapter, it is probable that the muscles of the pharynx are supplied by filaments from the pneumogastric, which are originally derived from the spinal accessory.

Near the base of the tongue, branches are sent to the mucous membrane covering the tonsils and the soft palate.

The lingual branches penetrate the tongue about midway between its border and centre and are distributed to the mucous membrane at its base, being probably connected with the papillæ.

General Properties of the Glosso-Pharyngeal.—As in the case of other sensory nerves emerging from the cranial cavity, it is important, in studying the general properties of the glosso-pharyngeal, to make our observations under certain conditions. First, it must be remembered that this nerve contracts anastomoses a short distance from its origin. As we desire to know the properties of the original filaments of the nerve, we must operate upon it before it has received communicating fibres. Next, in irritating sensory nerves, we are liable to produce reflex contractions. To avoid this, the nerve must be divided, when the reflex contractions will only follow stimulation of the central end. It is probably from a neglect of these essential experimental conditions, that the results of direct observation have been so discordant in the hands of different physiologists.

To begin with, we shall assume that the glosso-pharyngeal nerve must be irritated between its origin and the ganglion of Andersch, in order to avoid anastomosing filaments from motor nerves, and that the nerve must be divided and irritation be applied to its peripheral end, to avoid reflex movements. Assuming these conditions as essential, we can discard most of the earlier experiments, as open to the objections we have mentioned. Longet, operating upon horses and dogs, after removal of the cerebral lobes and division of the glosso-pharyngeal, found that galvanization of the peripheral extremity of the nerve did not produce movements of the palate or pharynx; and, from these experiments, he concludes that the nerves are exclusively sensory at their roots, or, at least, that they do not contain motor filaments. In another chapter, under the head of movements of the palate and uvula, we have cited in detail a series of experiments which illustrate the reflex movements of the velum palati through the facial, produced by galvanization of the glosso-pharyngeal. As a complement to the first experiments of Longet, just cited, the same observer noted contractions of the pharyngeal muscles following galvanization of the peripheral end of the divided nerve in the neck, which could only be produced by the action of motor anastomosing filaments.

As regards general sensibility, there can be no doubt of the fact that the glosso-pharyngeal is sensory, although its sensibility is somewhat obtuse. In the experiments in which the nerve has seemed to be insensible to ordinary impressions, it is probable that the animals operated upon had been exhausted more or less by pain and loss of blood in the operation of exposing the nerve, which, it is well known, abolish the sensibility of some of the nerves. Longet states distinctly that, unless the animals (dogs) be already exhausted by resistance during the operation, they have always appeared to suffer pain on pinching or dividing the glosso-pharyngeal.

Experiments upon the glosso-pharyngeal are not very definite and satisfactory in their results as regards the general sensibility of the base of the tongue, the palate, and the pharynx. The sensibility of these parts seems to depend chiefly upon branches of the fifth passing to the mucous membrane through Meckel's ganglion. Experiments show, also, that the reflex phenomena of deglutition take place mainly through these branches of the fifth, and that the glosso-pharyngeal has little or nothing to do with the process. In fact, after division of both glosso-pharyngeal nerves, deglutition does not seem to be affected.

With these remarks, we dismiss the functions of the glosso-pharyngeals as nerves of general sensibility and shall consider in detail their relations to the sense of taste.

Relations of the Glosso-Pharyngeal Nerves to Gustation.—Relying upon experiments on the inferior animals, particularly dogs, it seems pretty certain that there are two nerves presiding over the sense of taste: The chorda tympani gives this sense to the anterior portion of the tongue exclusively, probably the anterior two-thirds; the glosso-pharyngeal supplies this sense to the posterior portion of the tongue; the chorda tympani seems to have nothing to do with general sensibility; while the glosso-pharyngeal is an ordinary sensory nerve, as well as a nerve of special sense.

Where there are such differences in the delicacy of the sense of taste as exist usually in different individuals, it must be difficult to describe with accuracy delicate shades of savor, particularly in alimentary substances; but the distinct impressions of acidity or bitter quality are easily recognizable. It is certain, however, that saline, acid, and styptic tastes are best appreciated through the chorda tympani, and that sweet, alkaline, bitter, and metallic impressions are received mainly by the glosso-pharyngeal.

Mechanism of Gustation.—The mode in which sapid substances are brought in contact with the organ of taste is so simple, that we need only allude to it, before we study the anatomy of the parts directly concerned and their connections with the terminal filaments of the gustatory nerves. In the first place, the articles which make the special impression are in solution; introduced into the mouth, they increase the flow of saliva, the reflex action involving chiefly the submaxillary and sublingual glands; there is usually more or less mastication, which increases the flow of the parotid saliva; and, during the acts of mastication and the first stages of deglutition, the sapid substances are distributed over the gustatory membrane, so much so, indeed, that it is difficult to exactly locate the seat ot the special impression. In this way, by the movements of the tongue, aided by an increased flow of saliva, the actual contact of the savory articles is rapidly effected. The thorough distribution of these substances over the tongue and the mucous membrane of the general buccal cavity leads to a certain amount of confusion in our appreciation of the special impressions; and, in order to ascertain if different portions of the membrane possess different properties, it is necessary to make careful experiments, limiting the points of contact as closely as possible. This has been done, with the result of showing that the true gustatory organ is quite restricted in its extent, and, as such, it demands special anatomical description.

Physiological Anatomy of the Organ of Taste.—Recent anatomical and physiological researches have shown that, at least in the human subject, the organ of taste is probably confined to the dorsal surface of the tongue. When we examine the structure of the mucous membrane of the mouth, tongue, and palate, we find that the upper surface of the tongue presents numerous papillæ, called, in contradistinction to the filiform papillæ, fungiform and circumvallate. These are not found on its under surface or anywhere except on the superior portion. It is now pretty well established that the circumvallate and fungiform papillæ alone are the organs of taste. Camerer, in some recent experiments upon the gustatory organs by the application of solutions to different parts through fine glass tubes, concluded that the parts around a papilla have no gustatory sensibility, but that different savors can be distinguished when a single papilla is touched. These observations give a new importance to the peculiar papillæ of the tongue, and we therefore present a description of their arrangement and structure.

In Fig. 236, which represents the dorsal surface of the tongue, the large, circumvallate papillæ, which usually number from seven to twelve, are seen in the form of a V, occupying the base of the tongue. The fungiform papillæ are scattered over the surface but are most numerous at the point and near the borders. Both of these varieties of papillæ are distinguishable by the naked eye.

The circumvallate papillæ are simply enlarged fungiform papillæ, each one surrounded by a circular ridge, or wall, and covered by numerous small, secondary papillæ. The fungiform papillæ have a short, thick pedicle and enlarged, rounded extremities. According

FIG. 236.—*Papillæ of the tongue.* (Sappey.)

1, 1, circumvallate papillæ; 2, median circumvallate papilla, which entirely fills the foramen cæcum; 3, 3, 3, 3, fungiform papillæ; 4, 4, filiform papillæ; 5, 5, vertical folds and furrows of the border of the tongue; 6, 6, 6, 6, glands at the base of the tongue; 7, 7, tonsils; 8, epiglottis; 9, median glosso-epiglottidean fold.

ing to Sappey, from one hundred and fifty to two hundred of these can easily be counted. These, also, present secondary papillæ on their surface. When the mucous membrane of the tongue is examined with a low magnifying power, particularly after maceration in acetic or dilute hydrochloric acid, their structure is readily observed. They are abundantly supplied with blood-vessels and nerves.

Taste-Buds, or Taste-Beakers.—A few years ago, Lovén and, a little later, Schwalbe described, under these names, peculiar structures, which are supposed to be the true organs of taste. They are found on the lateral slopes of the circumvallate papillæ and occasionally on the fungiform papillæ. The structure of these organs is very simple. They consist of flask-like collections of spindle-shaped cells, which are received into little excavations in the epithelial covering of the mucous membrane, the bottom resting upon the connective-tissue layer. Their form is ovoid, and, at the neck of the flask, is a

FIG. 237.

FIG. 238.

Varieties of papillæ of the tongue. (Sappey.)

Fig. 237.—Medium-sized circumvallate papilla: 1, papilla, the base only being apparent: it is seen that the base is covered with secondary papillæ; 2, groove between the papilla and the surrounding wall; 3, 3, wall of the papilla.
Fig. 238.—Fungiform, filiform, and hemispherical papillæ: 1, 1, two fungiform papillæ, covered with secondary papillæ; 2, 2, 2, filiform papillæ; 3, a filiform papilla, the prolongations of which are turned outward; 4, a filiform papilla, with vertical prolongations; 5, 5, small filiform papillæ, with the prolongations turned inward; 6, 6, filiform papillæ, with striations at their bases; 7, 7, hemispherical papillæ, slightly apparent, situated between the fungiform and the filiform papillæ.

rounded opening, called the taste-pore. Their length is from $\frac{1}{350}$ to $\frac{1}{800}$, and their transverse diameter, about $\frac{1}{600}$ of an inch. The cavity of the taste-beakers is filled with cells, of which two kinds are described. The first variety, the outer cells, or the cover-cells, are spindle-shaped, and curved to correspond to the wall of the beaker. These come to a point at the taste-pore. In the interior of the beaker, are elongated cells, with large, clear nuclei, which are called taste-cells. It is supposed that nerve-fibrils are connected directly with these cells. As far as we can learn, the only reason why these structures are connected with the physiology of gustation is on account of their anatomical relations to the gustatory papillæ.

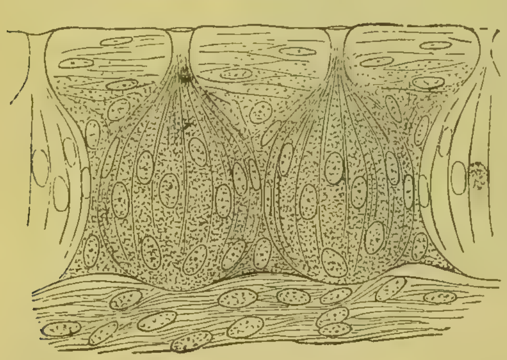


FIG. 239.—*Taste-buds from the lateral taste-organ of the rabbit.* (Engelmann.)

It now remains only to note the ultimate distribution of the nerves in the gustatory organ. Upon this point, anatomical researches are not entirely satisfactory. However, the following description, by Elin, may be regarded as probably correct, although the facts have not been absolutely demonstrated. According to this authority, from the submucous tissue, small nerve-branches pass perpendicularly to the upper layer of the membrane. These fibres have a varicose appearance. In the most superficial layer of the mucous membrane, there is a net-work of fine, non-medullated fibres; and, from this net-work, branches follow the blood-vessels into the papillæ and penetrate the epithelium. Sometimes, though more seldom, they pass into the epithelium lying between the papillæ. In this layer, there are branches which end, some in nerve-cells, and some taking a winding course and passing into neighboring fibres. These descriptions are from preparations made with chloride of gold; but the plates by which they are illustrated are somewhat unsatisfactory.

According to the views of those who have described the so-called taste-beakers, sapid solutions find their way into the interior of these structures through the taste-pores and come in contact with what have been called the taste-cells, these structures being directly connected with the terminal filaments of the gustatory nerves.

CHAPTER XXIV.

VISION.

General considerations—Physiological anatomy and general properties of the optic nerves—Physiological anatomy of the eyeball—Sclerotic coat—Cornea—Membrane of Descemet, or of Demours—Ligamentum iridis pectinatum—Choroid coat—Ciliary processes—Ciliary muscle—Iris—Pupillary membrane—Retina—Crystalline lens—Aqueous humor—Chambers of the eye—Vitreous humor—Summary of the anatomy of the globe—The eye as an optical instrument—Laws of refraction, dispersion, etc., bearing upon the physiology of vision—Theories of light—Refraction by lenses—Myopia and hypermetropia—Formation of images in the eye—Mechanism of refraction in the eye—Astigmatism—Movements of the iris—Direct action of light upon the iris—Action of the nervous system upon the iris—Mechanism of the movements of the iris—Accommodation of the eye to vision at different distances—Changes in the crystalline lens in accommodation—Action of the ciliary muscle—Changes in the iris in accommodation—Erect impressions produced by images inverted upon the retina—Single vision with both eyes—Corresponding points—The horopter—Appreciation of distance and of the form of objects—Mechanism of the stereoscope—Duration of luminous impressions—Irradiation—Movements of the eyeball—Muscles of the eyeball—Parts for the protection of the eyeball—Eyelids—Muscles which open and close the eyelids—Conjunctival mucous membrane—Lachrymal apparatus—Composition of the tears.

The chief important points to be considered in the physiology of vision are the following:

1. The physiological anatomy and the general properties of the optic nerves.
2. The physiological anatomy of the parts essential to correct vision.
3. The laws of refraction, diffusion, etc., bearing upon the physiology of vision.
4. The action of the different parts of the eye in the production and appreciation of correct images.
5. Binocular vision.
6. The physiological anatomy and the functions of accessory parts, as the muscles which move the eyeball.
7. The physiological anatomy and the functions of the parts which protect the eye, as the lachrymal glands, eyelids, etc.

Physiological Anatomy of the Optic Nerves.—The optic nerves, or optic tracts, take their origin, each by two principal roots of white matter and a few filaments from what is described as the gray root, chiefly from the tubercula quadrigemina, but in part from those portions of the encephalon over which the nerves pass to go to the eyes. The internal white root arises from the posterior, and the external white root, which is the larger, from the anterior tuberculum. The gray root is situated in front of and above the optic commissure and is a dependence of the gray matter which covers the internal surface of the optic thalamus. It arises from the gray matter which constitutes the anterior floor of the third ventricle, in the form of delicate filaments which join the optic nerves at this point.

The apparent origin of the optic nerves is from the tubercula quadrigemina, receiving filaments from the corpora geniculata, the optic thalami, the peduncles of the cerebrum, the anterior substantia perforata, the tuber cinereum, and the lamina terminalis. It has thus far been found impossible to trace all these roots to their true origin in the cerebral substance; but experiments upon the lower animals, in which it has been shown that the sense of sight is completely abolished by destruction of the tubercula quadrigemina (called bigemina, in birds), show that the origin of the filaments that preside over vision is, in all probability, from these bodies.

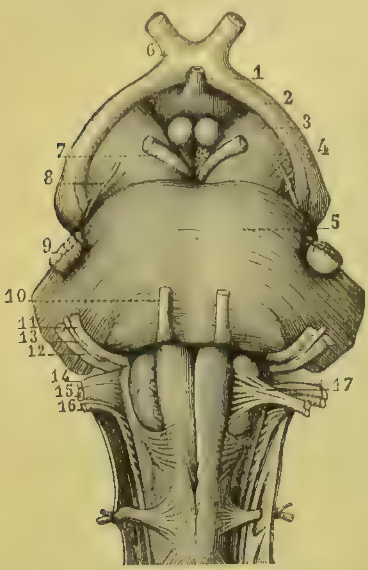


FIG. 240.—*Optic tracts, commissure, and nerves.* (Hirschfeld.)

1, infundibulum; 2, *corpus cinereum;* 3, corpora albicantia; 4, *cerebral peduncle;* 5, tuber annulare; 6, *optic tracts and nerves, decussating at the commissure, or chiasm;* 7, motor oculi communis; 8, patheticus; 9, fifth nerve; 10, motor oculi externus; 11, facial nerve; 12, auditory nerve; 13, nerve of Wrisberg; 14, glosso-pharyngeal nerve; 15, pneumogastric; 16, spinal accessory; 17, sublingual nerve.

The two principal roots of the optic nerves unite above the external corpus geniculatum, forming a flattened band, which takes an oblique course around the under surface of the crus cerebri to the optic commissure. This is usually called the optic tract, in contradistinction to the optic nerve, which is described as arising from the optic commissure.

The optic commissure, or chiasm, is situated just in front of the corpus cinereum, resting upon the olivary process of the sphenoid bone. As its name implies, this is the point of union between the nerves of the two sides. At the commissure, the fibres from the optic tracts take three directions; and, in addition, the commissure contains filaments passing from one eye to the other, which have no connection with the optic tracts. The four sets of fibres in the optic commissure are the following:

1. Decussating fibres, passing from the optic tract upon either side to the eye of the opposite side. The greatest part of the fibres take this direction. Their relative situation is internal.

2. External fibres, much less numerous than the preceding, which pass from the optic tract to the eye upon the same side.

3. Fibres, situated on the posterior boundary of the commissure, which pass from one optic tract to the other and do not go to the eyes. These fibres are scanty and are sometimes wanting.

4. Fibres, situated on the anterior border of the commissure, more numerous than the preceding, which pass from one eye to the other and which have no connection with the optic tracts.

It is probable, reasoning chiefly from cases of cerebral injury or disease, that the filaments from the optic tracts upon the two sides are connected with distinct portions of the retina; and two pathological cases have lately been reported by Drs. Keen and Thomson, of Philadelphia, which go to show that this is the fact, and which illustrate certain interesting points in connection with the decussation of the nerves. One was a case of gunshot-wound of the head, with severe injury of the brain-substance. This case presented, immediately after the injury, unconsciousness and partial paralysis of the right arm and right leg, which lasted two or three months. About a year after, the paralysis had almost entirely disappeared, but the memory was somewhat impaired. Upon careful examination of the eyes, it was ascertained that the field of vision was divided in each eye by a vertical line passing through its centre. In the right eye, the inner half of the retina, beginning on a line with the inner border of the macula lutea, was entirely insensible to light. In the left eye, the outer half of the retina, beyond the macula, was insensible to light. No pathological appearances were observed upon examining the retinæ with the ophthalmo-

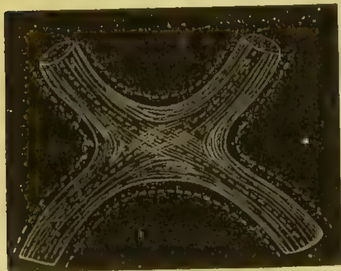


FIG. 241.—*Diagram of the decussation at the optic commissure.* The dotted lines show the four directions of the fibres.

scope. The second case, reported by Dr. W. Thomson, presented the same condition following partial hemiplegia, the result of sunstroke. The peculiar affection of vision in these cases, called hemiopsia, especially as illustrated in the first case, reported by Dr. Keen, can be explained by assuming the following as the course of the decussating fibres of the optic tracts: From the left side of the encephalon, visual fibres pass to the right eye, supplying the inner mathematical half of the retina, from a vertical line passing through the macula lutea. Visual fibres also pass to the left eye, supplying the outer half of the retina, beginning at the macula lutea. The macula lutea, then, and not the point of entrance of the optic nerve, is in the line of division of the visual field. The outer half of the left and the inner half of the right retina are supplied by fibres from the left side; and the outer half of the right and the inner half of the left retina are supplied from the right side. Although this anatomical arrangement has not been actually demonstrated, it is rendered exceedingly probable by pathological cases like those just cited. In the case reported by Dr. Keen, the left side of the brain was injured, as the paralysis occurred in the right leg and arm.

With the exception of the few filaments derived from what have been described as the gray roots, the fibres of the optic tracts and the optic nerves are of the medullated variety, and they present no differences in structure from the ordinary cerebro-spinal nerves.

The optic commissure is covered with a fibrous membrane and is consequently more resisting than the optic tracts. From its anterior and outer border, arise the optic nerves, which take a curved direction to the eyes. The nerves are rounded and are enclosed in a double fibrous sheath derived from the dura mater and the arachnoid. They pass into the orbit upon the two sides by the optic foramina and penetrate the sclerotic at the posterior, inferior, and internal portion of the globe. As the nerves enter the globe, they lose their coverings from the dura mater and arachnoid. The sheath derived from the dura mater is adherent to the periosteum of the orbit at the foramen opticum, and, when it reaches the globe, it fuses with the sclerotic coat. Just before the nerves penetrate the globe, they each present a well-marked constriction. At the point of penetration, there is a thin but strong membrane, presenting numerous perforations for the passage of the nervous filaments. This membrane, the lamina cribrosa, is in part derived from the sclerotic, and in part, from the coverings of the individual nerve-fibres, which lose their investing membranes at this point. In the interior of each eye, there is a little, mammillated eminence, formed by the united fibres of the nerve. The retina, with which the optic nerve is connected, will be described as one of the coats of the eye.

In the centre of the optic nerve, is a minute canal, lined by fibrous tissue, in which are lodged the central artery of the retina and its corresponding vein, with a delicate nervous filament from the ophthalmic ganglion. The vessels penetrate the optic nerve a short distance (from $\frac{1}{5}$ to $\frac{4}{5}$ of an inch) behind the globe. The central canal does not exist behind these vessels.

General Properties of the Optic Nerves.—There is very little to be said regarding the general properties of the optic nerves, except that they are undoubtedly the only nerves capable of conveying to the cerebrum the special impressions of sight, and that they are not endowed with general sensibility.

That the optic nerves are the only nerves of sight, there can be no doubt. Their division or injury always involves loss or impairment of vision, directly corresponding with the lesion. It is interesting, however, to note that they are absolutely insensible to ordinary impressions. "We can, in a living animal, pinch, cauterize, cut, destroy in any way the optic nerve without giving rise to the slightest painful sensation; whether it be taken before or after its decussation, it seems completely insensible in its entire length." (Longet.)

Not only are the optic nerve and retina insensible to pain, but any irritation produces the impression of light. This was stated in the remarkable paper, *Idea of a New Anatomy* *of the Brain*, printed by Charles Bell, in 1811. A few years later, Magendie, in operating for cataract, passed the needle to the bottom of the eye and irritated the retina, in two persons. The patients experienced no pain but merely an impression of flashes of light. The insensibility of the optic nerves has also been repeatedly noted in surgical operations in which the nerves have been exposed. If a current of galvanism be passed through the optic nerves, a sensation of light is experienced. The same phenomenon is observed when the eyeball is pressed upon or contused, a fact which is sufficiently familiar.

Physiological Anatomy of the Eyeball.

The eyeball is a spheroidal body, partially embedded in a cushion of fat in the orbit, protected by the surrounding bony structures and the eyelids, its surface bathed by the secretion of the lachrymal gland, and movable in various directions by the action of certain muscles. When the axis of the eye is directed forward, the globe has the form of a sphere in its posterior five-sixths, with the segment of a smaller sphere occupying its anterior sixth. The segment of the smaller sphere, bounded externally by the cornea, is more prominent than the rest of the surface.

The eyeball is made up of several coats enclosing certain refracting media. The external coat is the sclerotic, covering the posterior five-sixths of the globe, which is continuous with the cornea, covering the anterior sixth. This is a dense, opaque, fibrous membrane, for the protection of the inner coats and the contents of the globe. The cornea is dense, resisting, and perfectly transparent. The muscles that move the globe of the eye are attached to the sclerotic coat.

Were it not for the prominence of the cornea, the eyeball would present very nearly the form of a perfect sphere, as will be seen by the following measurements of its various diameters; but the prominence of its anterior sixth gives the greatest diameter in the antero-posterior direction.

The form and dimensions of the globe are subject to considerable variations after death, by evaporation of the humors, emptying of vessels, etc., and there is no way in which the normal conditions can be restored. The most exact measurements are those made by Sappey. As an illustration of the post-mortem changes in the eye, Sappey mentions comparative measurements made three hours and twenty-four hours after death, the results of which presented very considerable differences.

In measurements made by Sappey, apparently with great care and accuracy, from one to four hours after death, of the eyes of twelve adult females and fourteen adult males of different ages, the following mean results were obtained:

Subjects examined.	Diameters (Inch).			
	Ant.-post.	Transverse.	Vertical.	Oblique.
Mean of 12 females, from 18 to 81 years of age	0·941	0·911	0·905	0·937
Mean of 14 males, from 20 to 79 years of age	0·968	0·941	0·925	0·949

From these results, it is seen that all the diameters are less in the female than in the male. The antero-posterior diameter is the greatest of all, and the vertical diameter is the shortest. The measurements at different ages, not cited in the table just given, show that the excess of the antero-posterior diameter over the others is diminished by age.

Sclerotic Coat.—The sclerotic is the dense, opaque, fibrous covering of the posterior five-sixths of the eyeball. Its thickness is different in different portions. At the point of penetration of the optic nerve, it measures $\frac{1}{25}$ of an inch. It is thinnest at the middle portion of the eye, measuring about $\frac{1}{50}$ of an inch, and is a little thicker again near the cornea. This membrane is composed chiefly of bundles of ordinary connective tissue.

The fibres are slightly wavy, and arranged in flattened bands, which are alternately longitudinal and transverse, giving the membrane a lamellated appearance, although it cannot be separated into distinct layers. Mixed with these bands of connective-tissue fibres, are numerous small fibres of elastic tissue. The vessels of the sclerotic are scanty. They are derived from the ciliary vessels and the vessels of the muscles of the eyeball. The tissue of the sclerotic yields gelatine on boiling.

Cornea.—The cornea is the transparent membrane which covers about the anterior sixth of the globe of the eye. As before remarked, this is the most prominent portion of the eyeball. It is in the form of a segment of a sphere attached by its borders to the segment of the larger sphere formed by the sclerotic. The thickness of the cornea is about $\frac{1}{30}$ of an inch in its central portion, and about $\frac{1}{25}$ of an inch near its periphery. Its substance is composed of transparent fibres, arranged in incomplete layers, something like the layers of the sclerotic. It yields chondrine, instead of gelatine, on boiling.

Upon the external, or convex surface of the cornea, are several layers of delicate, transparent, nucleated epithelium. The most superficial cells are flattened, the middle cells are rounded, and the deepest cells are elongated and arranged perpendicularly. These cells become slightly opaque and whitish after death. Just beneath the epithelial covering of the cornea, is a very thin, transparent membrane, described by Bowman under the name of the "anterior elastic lamella." This membrane, with its cells, is a continuation of the conjunctiva.

The proper corneal membrane is composed of excessively pale, flattened bundles of fibres, interlacing with each other in every direction. Their arrangement is lamellated, although they cannot be separated into complete and distinct layers. Between the bundles of fibres, lie a great number of stellate, anastomosing, connective-tissue corpuscles. In these cells and in the intervals between the fibres, there is a considerable quantity of transparent liquid. The fibres constituting the substance of the cornea are continuous with the fibrous structure of the sclerotic, from which they cannot be separated by maceration. At the margin of the cornea, the opaque fibres of the sclerotic abruptly become transparent. The corneal substance is very tough, and it will resist a pressure sufficient to rupture the sclerotic.

Upon the posterior, or concave surface of the cornea, is the membrane of Descemet, or of Demours. This is elastic, transparent, structureless, rather loosely attached, and covered with a single layer of regularly polygonal, nucleated epithelium. At the circumference of the cornea, a portion of this membrane passes to the anterior surface of the iris, in the form of numerous processes which constitute the ligamentum iridis pectinatum, a portion passes into the substance of the ciliary muscle, and a portion is continuous with the fibrous structure of the sclerotic.

In the adult, the cornea is almost without blood-vessels, but in fœtal life it presents a rich plexus extending nearly to the centre. These disappear, however, before birth, leaving a very few delicate, looped vessels at the extreme edge.

A great deal of anatomical interest has lately been attached to the cornea, from researches showing the termination of the fine nerve-fibres in the nuclei of the posterior layer of the epithelium of its convex surface and the investigation of the "lymph-spaces" by the use of certain reagents, the demonstration of the so-called "wandering cells," etc., points that we do not propose to consider. It is well known that the surface of the cornea is exquisitely sensitive.

Choroid Coat.—Calling the sclerotic and the cornea the first coat of the eyeball, the second is the choroid, with the ciliary processes, the ciliary muscle, and the iris. This was called by the older anatomists the uvea, a name which was later applied, sometimes to the entire iris, and sometimes to its posterior, or pigmentary layer. We shall describe, however, the choroid and ciliary processes together as the second coat, and then take up the ciliary muscle and the iris.

The choroid is distinguished from the other coats of the eye by its dark color and its great vascularity. It occupies that portion of the eyeball corresponding to the sclerotic. It is perforated posteriorly by the optic nerve and is connected in front with the iris. It is very delicate in its structure and is composed of two or three distinct layers. Its thickness is from $\frac{1}{150}$ to $\frac{1}{25}$ of an inch. Its thinnest portion is at about the middle of the eye. Posteriorly it is a little thicker. Its thickest portion is at its anterior border.

The external surface of the choroid is connected with the sclerotic by vessels, nerves (the long ciliary arteries and the ciliary nerves), and very loose connective tissue. This is sometimes called the membrana fusca, although it can hardly be called a distinct layer. It contains, in addition to the vessels, nerves, and fibrous tissue, a few irregularly-shaped pigment-cells.

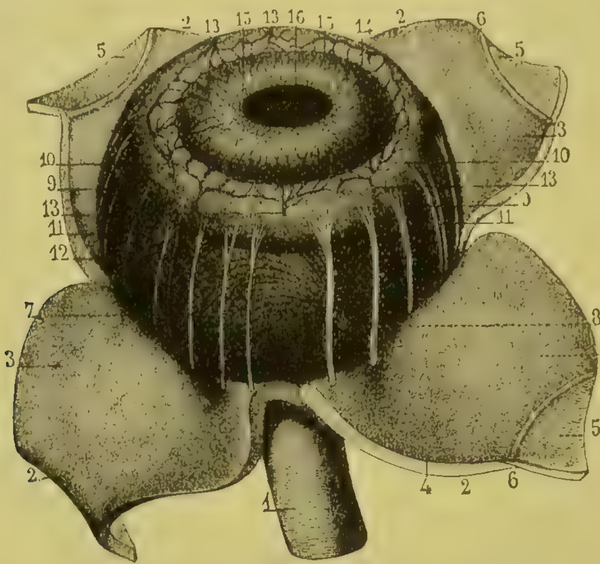


FIG. 242.—*Choroid coat of the eye.* (Sappey.)

1, optic nerve; 2, 2, 2, 2, 3, 3, 3, 4, sclerotic coat, divided and turned back to show the choroid; 5, 5, 5, 5, the cornea divided into four portions and turned back; 6, 6, canal of Schlemm; 7, external surface of the choroid, traversed by the ciliary nerves and one of the long ciliary arteries; 8, central vessel into which open the vasa vorticosa; 9, 9, 10, 10, choroid zone; 11, 11, ciliary nerves; 12, long ciliary artery; 13, 13, 13, 13, anterior ciliary arteries; 14, iris; 15, 15, vascular circle of the iris; 16, pupil.

The rest of the choroid is composed of two distinct layers; viz., an external, vascular, and an internal, pigmentary layer. The vascular layer consists of numerous arteries, veins, and capillaries, arranged in a peculiar manner. The layer of capillary vessels, which is internal, is sometimes called the middle layer of the choroid, or the tunica Ruyschiana. The arteries, which are derived from the posterior short ciliary arteries and are connected with the capillary plexus, lie just beneath the pigmentary layer. The plexus of capillaries is closest at the posterior portion of the membrane. The veins are external to the other vessels. They are very numerous and are disposed in curves converging to four trunks. This arrangement gives the veins a very peculiar appearance, and they have been called the vasa vorticosa. The pigmentary portion is composed, over the greatest part of the choroid, of a single layer of regularly polygonal cells, somewhat flattened, measuring from $\frac{1}{2000}$ to $\frac{1}{1500}$ of an inch in diameter. These cells are filled with pigmentary granulations of uniform size, and they give to the membrane its characteristic dark-brown or chocolate color. The pigmentary granules in the cells are less numerous near their centre, where a clear nucleus can readily be observed. In the anterior portion of the membrane, in front of the anterior limit of the retina, the cells are smaller, more rounded, more completely filled with pigment, and present several layers. Beneath the layer of hexagonal pigment-cells, the intervascular spaces of the choroid are occupied by stellate pigment-cells.

Ciliary Processes.—The anterior portion of the choroid is arranged in the form of folds or plaits projecting internally, called the ciliary processes. The largest of these folds are about $\frac{1}{10}$ of an inch in length. They are from sixty to eighty in number. The larger folds are of nearly uniform size and are regularly arranged around the margin of the crystalline lens. Between these folds, which constitute about two-thirds of the entire number, are smaller folds, lying, without any regular alternation, between the larger. Within the folds, are received corresponding folds of the thick membrane, continuous anteriorly with the hyaloid membrane of the vitreous humor, called the zone of Zinn.

The ciliary processes present blood-vessels, which are somewhat larger than those of the rest of the choroid. The pigmentary cells are smaller and are arranged in several layers. The anterior border of the processes is free and contains little or no pigment.

Ciliary Muscle.—This muscle, formerly known as the ciliary ligament and now sometimes called the tensor of the choroid, is almost universally recognized by physiologists as the agent for the accommodation of the eye to vision at different distances. Under this view, the ciliary muscle is an organ of great importance, and it is essential, in the study of accommodation, to have an exact idea of its relations to the coats of the eye and to the crystalline lens. For this reason, we shall describe its arrangement as exactly as possible.

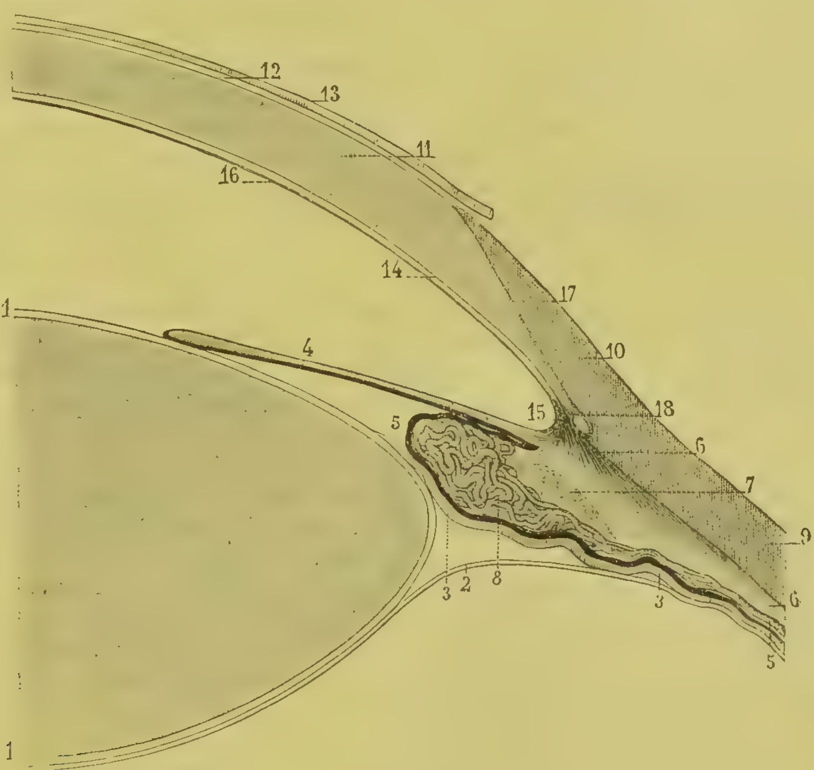


FIG. 243.—*Ciliary muscle; magnified 10 diameters.* (Sappey.)

1, 1, crystalline lens; 2, hyaloid membrane; 3, zone of Zinn; 4, iris; 5, 5, one of the ciliary processes; 6, 6, radiating fibres of the ciliary muscle; 7, section of the circular portion of the ciliary muscle; 8, venous plexus of the ciliary process; 9, 10, sclerotic coat; 11, 12, cornea; 13, epithelial layer of the cornea; 14, membrane of Descemet; 15, ligamentum iridis pectinatum; 16, epithelium of the membrane of Descemet; 17, union of the sclerotic coat with the cornea; 18, section of the canal of Schlemm.

The form and situation of the ciliary muscle are as follows: It surrounds the anterior margin of the choroid, in the form of a ring about $\frac{1}{8}$ of an inch wide and $\frac{1}{50}$ of an inch in thickness at its thickest portion, which is its anterior border. It becomes thinner from before backward, until its posterior border apparently fuses with the fibrous structure of the choroid. It is semitransparent and of a grayish color. Its situation is just outside of the ciliary processes, these processes projecting in front of its anterior border about $\frac{1}{25}$ of an inch. Regarding the anterior border of this muscle as its origin and the posterior border as its insertion, it arises in front from the circular line of junction of the cornea and sclerotic, from the border of the membrane of Descemet, and the ligamentum iridis pectinatum. Its fibres, which are chiefly longitudinal, pass backward and are lost in the choroid, extending somewhat farther back than the anterior limit of the retina. In addition, a net-work of circular muscular fibres has been described lying over the anterior portion of the ciliary body, at the periphery of the iris, beneath the longitudinal fibres. Some of these fibres have an oblique direction.

Although there was formerly considerable discussion with regard to the structure of the ciliary ligament, or muscle, there can now be scarcely any doubt of the fact that it is composed mainly of muscular fibres. These fibres, anatomically considered, belong to the non-striated, or involuntary variety. They are pale, present numerous oval, longitudinal nuclei, and have no striæ.

It is evident, from the arrangement of the fibres of the ciliary muscle, that its action must be to approximate the border of connection of the sclerotic and cornea and the circumference of the choroid, compressing the vitreous humor and relaxing the suspensory ligament of the crystalline lens. We shall see farther on that this action enables the lens to change its form, and probably it adapts the curvature of the lens to vision at different distances. The nerves of the ciliary muscle are derived from the long and the short ciliary.

Iris.—The iris corresponds to the diaphragm of optical instruments, except that its orifice is capable of dilatation and contraction. It is a circular membrane, situated just in front of the crystalline lens, with a round perforation, the pupil, near its centre. It is called the uvea by some anatomists, a name that was formerly applied to the iris and choroid together.

The attachment of the greater circumference of the iris is to the line of junction of the cornea and sclerotic, near the origin of the ciliary muscle, the latter passing backward to be inserted into the choroid, and the former passing directly over the crystalline lens. The diameter of the iris is about half an inch. The pupil is subject to considerable variations in size. When at its medium of dilatation, the diameter of the pupil is from $\frac{1}{8}$ to $\frac{1}{6}$ of an inch. The pupillary orifice is not in the mathematical centre of the iris but is situated a little toward the nasal side. The thickness of the iris is a little greater than that of the choroid, but it is unequal in different parts, the membrane being thinnest at its great circumference and its pupillary border, and thickest at about the junction of its inner third with the outer two-thirds. It slightly projects anteriorly and divides the space between the lens and the cornea into two chambers, anterior and posterior, the anterior chamber being much the larger. Taking advantage of a property of the crystalline lens, called fluorescence, which enables us, by concentrating upon it a blue light, to see the boundaries in the living eye, Helmholtz has demonstrated that the posterior surface of the iris and the anterior surface of the lens are actually in contact, except, perhaps, for a certain distance near the periphery of the iris. This being the case, the posterior chamber is very small and only exists near the margins of the lens and the iris.

The color of the iris is very different in different individuals. Its anterior surface is generally very dark near the pupil and presents colored radiations toward its periphery. Its posterior surface is of a dark-purple color and is covered with pigmentary cells.

The entire iris presents three layers. The anterior layer is continuous with the membrane of the aqueous humor. At the great circumference, it presents little fibrous prolongations, forming a delicate dentated membrane, called the ligamentum iridis pectinatum. The membrane covering the general anterior surface of the iris is extremely thin and is covered by cells of tessellated epithelium. Just beneath this membrane, are a number of irregularly-shaped pigmentary cells.

The posterior layer of the iris is very thin, easily detached from the middle layer, and contains numerous small cells exceeding rich in pigmentary granules. Some anatomists recognize this membrane only as the uvea.[1]

The middle layer constitutes by far the greatest part of the substance of the iris. It is composed of connective tissue, muscular fibres of the non-striated variety, numerous blood-vessels, and, probably, nerve-terminations. From a physiological point of view, the arrangement of the muscular fibres is the most interesting. Directly surrounding the pupil, forming a band about $\frac{1}{48}$ of an inch in width, is a layer of non-striated muscular fibres, called the sphincter of the iris. The existence of these fibres is admitted by all anatomists. It is different, however, for the radiating muscular fibres. Most anatomists describe, in addition to the sphincter, fibres of the same variety, which can be traced from near the great circumference of the iris almost to its pupillary border, lying both in front of and behind the circular fibres, which are, as it were, enclosed between them. A few observers deny that these fibres are muscular; but they recognize a thick muscular layer surrounding the arteries of the iris. This is merely a question of observation; but the weight of anatomical authority is greatly in favor of the existence of the radiating fibres, and their presence explains certain of the phenomena of dilatation of the iris which would otherwise be difficult to understand.

The blood-vessels of the iris are derived from the arteries of the choroid, from the long posterior ciliary, and from the anterior ciliary arteries. The long ciliary arteries are two branches, running along the sides of the eyeball between the sclerotic and choroid, to form, finally, a circle surrounding the iris. The anterior ciliary arteries are derived from the muscular branches of the ophthalmic. They penetrate the sclerotic a little behind the iris and join the long ciliary arteries in the vascular circle. From this circle, the vessels branch and pass into the iris, to form a smaller arterial circle around the pupil. The veins from the iris empty into a circular sinus situated at the junction of the cornea with the sclerotic. This is sometimes spoken of as the circular venous sinus, or the canal of Schlemm.

The nerves of the iris are the long ciliary, from the fifth cranial, and the short ciliary, from the ophthalmic ganglion.

Pupillary Membrane.—At a certain period of fœtal life, the pupil is closed by a membrane connected with the lesser circumference of the iris, called the pupillary membrane. This is not distinct during the first months; but, between the third and the fourth months, it is readily seen. It is most distinct at the sixth month. The membrane is thin and transparent, and it completely separates the anterior from the posterior chamber of the eye. It is provided with vessels derived from the arteries of the iris, anastomosing with each other and turning back in the form of loops near the centre. At about the seventh month, it begins to give way at the centre, gradually atrophies, and generally scarcely a trace of it can be seen at birth.

Retina.—The retina is described by anatomists as the third tunic of the eye. It is closely connected with the optic nerve, and the most important structures entering into its composition are probably continuous with prolongations from the nerve-cells. This is the membrane endowed with the special sense of sight, the other structures in the eye being accessory.

If the sclerotic and choroid be removed from the eye under water, the retina is seen, in perfectly fresh specimens, in the form of an exceedingly delicate and transparent membrane covering the posterior portion of the vitreous humor. A short time after death, it becomes slightly opaline. It extends over the posterior portion of the eyeball to a dis-

[1] The name uvea was applied, at one time, to the choroid with the iris, again to the iris alone, and again to the posterior, or pigmentary layer of the iris. To avoid confusion, this term will not be again used.

tance of about $\frac{1}{15}$ of an inch behind the ciliary processes. When torn from its anterior attachment, it presents a finely-serrated edge, called the ora serrata. This edge adheres very closely, by mutual interlacement of fibres, to the zone of Zinn. In the middle of the membrane, its thickness is about $\frac{1}{120}$ of an inch. It becomes thinner near the anterior margin, where it measures only about $\frac{1}{300}$ of an inch. Its external surface is in contact with the choroid, and its internal, with the hyaloid membrane of the vitreous humor.

The optic nerve penetrates the retina about $\frac{1}{8}$ of an inch within and $\frac{1}{12}$ of an inch below the antero-posterior axis of the globe, presenting, at this point, a small, rounded elevation upon the internal surface of the membrane, perforated in its centre for the passage of the central artery of the retina. At from $\frac{1}{12}$ to $\frac{1}{8}$ of an inch external to the point of penetration of the nerve, is an elliptic spot, its long diameter being horizontal, about $\frac{1}{8}$ of an inch long and $\frac{1}{30}$ of an inch broad, called the yellow spot of Sömmerring, or the macula lutea. In the centre of this spot, is a depression, called the fovea centralis. This depression is exactly in the axis of distinct vision. The yellow spot exists only in man and the quadrumana.

The structures in the retina which present the greatest physiological interest are the external layer, formed of rods and cones, the layer of nerve-cells, and the filaments which connect the rods and cones with the cells. These are the only anatomical elements of the retina, as far as we know, that are directly concerned in the reception of optical impressions, and they will be described rather minutely, while the intermediate layers will be considered more briefly.

Most modern anatomists recognize eight distinct layers in the retina, as follows:

1. An external layer, situated next the choroid, called Jacob's membrane, the bacillar membrane, or the layer of rods and cones.
2. The external granule-layer.
3. The inter-granule layer (cone-fibre plexus, of Hulke).
4. The internal granule-layer.
5. The granular layer.
6. The layer of nerve-cells (ganglion-layer).
7. The expansion of the fibres of the optic nerve.
8. The limitary membrane.

The layer of rods and cones is composed of rods, or cylinders, extending through its entire thickness, closely packed, and giving to the external surface a regular, mosaic appearance; and, between these, are a greater or less number of flask-shaped bodies, the cones. This layer is about $\frac{1}{350}$ of an inch in thickness at the middle of the retina; $\frac{1}{400}$ of an inch, about midway between the centre and the periphery; and, near the periphery, about $\frac{1}{450}$ of an inch. At the macula lutea, the rods are wanting, and the layer is composed entirely of cones, which are here very much elongated. Over the rest of the membrane, the rods predominate, and the cones become less and less numerous toward the periphery.

The rods are regular cylinders, their length corresponding to the thickness of the layer, terminating above in truncated extremities, and below in points, which are probably continuous with the filaments of connection with the nerve-cells, though they have been actually traced only into the external granule-layer. Their diameter is about $\frac{1}{13000}$ of an inch. They are clear, of rather a fatty lustre, soft and pliable, but somewhat brittle, and so alterable that they are with difficulty seen in a natural state. They should be examined in perfectly fresh preparations, moistened with liquid from the vitreous humor or with serum. Their intimate structure, as well as that of the cones, has recently been very closely studied, especially by German anatomists. When perfectly fresh, it is difficult to make out any thing but an entirely homogeneous structure; but, shortly after death, each rod seems to be divided by a delicate line into an outer and an inner segment, the outer being a little the longer. At the upper extremity of the inner segment, is a hemispherical body, with its convexity presenting inward, called the lentiform body (*lin-*

senförmiger Körper). The entire inner segment is somewhat granular, and it often presents a granular nucleus at its inner extremity. The outer segment apparently differs in its constitution from the inner segment and is not similarly affected by reagents. Treated with dilute acetic acid, the outer segment becomes broken up transversely into thin disks. These points in the anatomy of the rods are referred to particularly, for the reason that they have lately been used as an anatomical basis for a theory of the perception of colors. They can be readily understood by reference to Fig. 244.

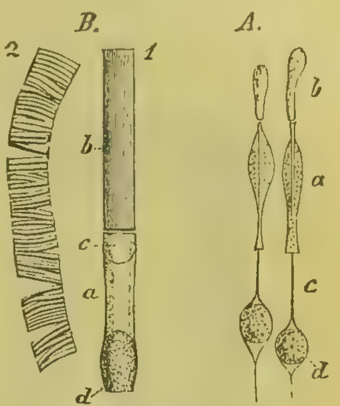


FIG. 244.—*Rods of the retina.* (Schultze.)

From the monkey.—*A.* Rods, after maceration in iodized serum, the outer segment (*b*) truncated, the inner segment (*a*) coagulated, granular, and somewhat swollen; *c*, filament of the rods; *d*, nucleus. *B.* Rods from the frog: 1. Fresh, magnified 500 diameters; *a*, inner segment; *b*, outer segment; *c*, lentiform body; *d*, nucleus. 2. Treated with dilute acetic acid and broken up into plates.

The cones are probably of the same constitution as the rods, but that portion called the inner segment is pyriform. The straight portion above (the outer segment) is sometimes called the cone-rod. The entire cones are about half the length of the rods and occupy the inner portion of the layer. The outer segment is, in its constitution, precisely like the outer segment of the rods. The inner segment is slightly granular and contains a nucleus. The cones are connected below with filaments passing into the deeper layers of the retina. The arrangement of the rods and cones is seen in Fig. 245, which shows the different layers of the retina.

At the fovea centralis, the external layer is composed entirely of immensely elongated cones, with no rods. These are slightly increased in thickness at the macula lutea, but are diminished again in thickness, by about one-half, at the fovea centralis. At the fovea, the optic nerve-fibres are wanting; and the ganglion-cells, which exist in a single layer over other portions of the retina, here present from six to eight layers, except at the very centre, where there are but three layers. Of the layers between the cones and the ganglion-cells, the external granule-layer and the inter-granule layer (cone-fibre plexus) remain, in the fovea, while the internal granule-layer and the granular (molecular) layer are wanting. At the fovea, indeed, those elements of the retina which may be regarded as purely accessory seem to disappear, leaving only the structures that are concerned directly in the reception of visual impressions.

The external granule-layer is composed of large granules, looking like cells, which are each nearly filled with a single nucleus. These are connected with the filaments from the rods and cones. They are rounded or ovoid and measure from $\frac{1}{12000}$ to $\frac{1}{6000}$ of an inch in diameter. The inter-granule layer (cone-fibre plexus) is composed apparently of minute fibrillæ and a few nuclei. The internal granule-layer is composed of cells nearly like those of the external granule-layer, but a little larger, and probably connected with the filaments of the rods and cones. The granular (molecular) layer is situated next the layer of ganglion-cells.

The layer of ganglion-cells is composed of multipolar cells, like those in the brain, measuring from $\frac{1}{3000}$ to $\frac{1}{750}$ of an inch in diameter. In the centre of the retina, at the macula lutea, the cells present eight layers, and they diminish to a single layer near the periphery. The smaller cells are situated near the centre, and the larger, near the periphery. Each cell sends off several filaments (from two to twenty-five) probably going to the layer of rods and cones, and a single filament, which becomes continuous with one of the filaments of the optic nerve.

The layer formed by the expansion of the optic nerve is composed of pale, transparent nerve-fibres, from $\frac{1}{50000}$ to $\frac{1}{25000}$ of an inch in diameter. These do not call for special description.

The limitary membrane is a delicate structure, with fine striæ and nuclei, composed of connective-tissue elements. It is about $\frac{1}{24000}$ of an inch in thickness. From this membrane, connective-tissue elements are sent into the various layers of the retina, where they form a framework for the support of the other structures.

As we before remarked, the retina becomes progressively thinner from the centre to the periphery. The granular layers and the nervous layers rapidly disappear in the anterior half of the membrane.

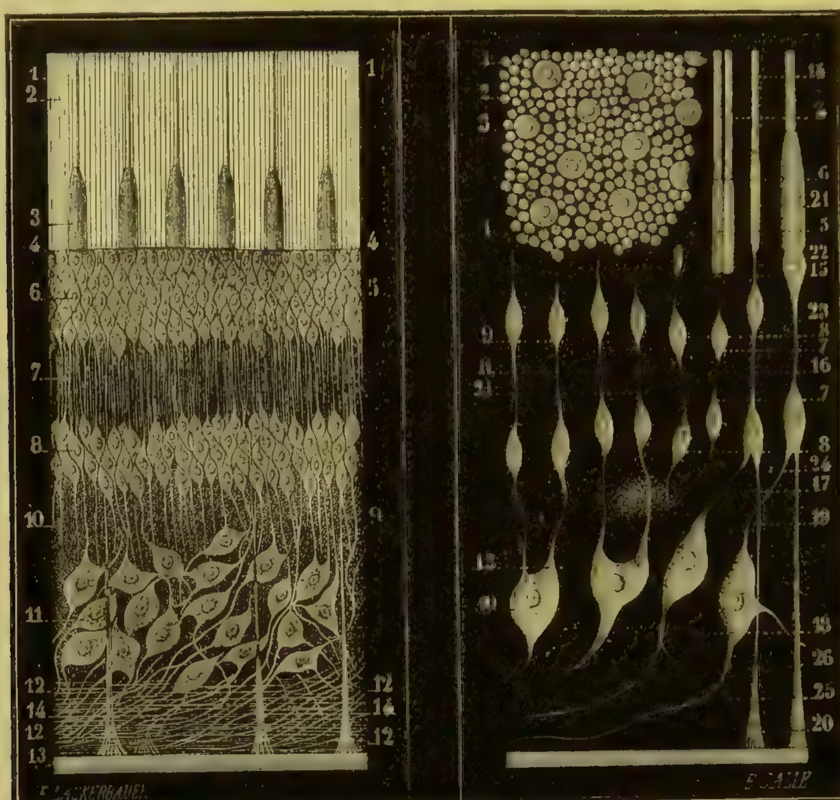


FIG. 245 (A).—*Vertical section of the retina.* (H. Müller.)

FIG. 245 (B).—*Connection of the rods and cones of the retina with the nervous elements.* (Sappey.)

FIG. 245 (A).—1, 1, layer of rods and cones; 2, rods; 3, cones; 4, 4, 5, 6, external granule-layer; 7, inter-granule layer (cone-fibre plexus); 8, internal granule-layer; 9, 10, finely granular gray layer; 11, layer of nerve-cells; 12, 12, 12, 12, 14, 14, fibres of the optic nerve; 13, membrana limitans.

FIG. 245 (B).—1, 1, 2, 3, rods and cones, front view; 4, 5, 6, rods, side view; 7, 7, 8, 8, cells of the external and internal granule-layers; 9, cell, connected by a filament with subjacent cells; 10, 13, nerve-cells, connected with cells of the granule-layers; 11, 21, filaments connecting cells of the external and internal granule-layers (12 is not in the figure); 14, 15, 16, 17, 18, 19, 20, 22, 23, 24, 25, 26, a rod and a cone, connected with the cells of the granule-layers, with the nerve-cells, and with the nerve-fibres.

The connection between the rods and cones and the ganglion-cells may be readily understood if we accept the following explanation: The filaments from the bases of the rods and cones pass inward, presenting, in their course, the corpuscles which we have described in the granule-layers, and finally become, as is thought, directly continuous with the poles of the ganglion-cells. The cells, in their turn, send filaments to the layer formed by the expansion of the optic nerve, which are continuous with the nerve-fibres. This arrangement is shown in Fig. 245 (B).

The arteries of the retina branch from the arteria centralis, presenting a beautifully arborescent appearance when viewed with the ophthalmoscope. They pass into the layer of gray nervous matter and send their branches to the periphery, where they supply a wide plexus of very small capillaries in the ora serrata. The capillaries empty into an incomplete venous circle, branches from which pass back by the sides of the arteries to the vena centralis. The macula lutea is provided with a rich plexus of minute capillaries.

Crystalline Lens.—The anatomy of the crystalline lens, as far as it bears upon the physiology of vision, is very simple. It is a double-convex lens, transparent, and exceedingly elastic. It has a function in the refraction of the rays of light analogous to the action of convex lenses in optical instruments. When we come to study its exact structure, however, we shall find many points that are still undetermined and somewhat obscure; but, fortunately, these are not, as far as we now know, of much physiological importance. In treating of the anatomy of the lens, we shall simply describe the most prominent and the well-determined points in its structure. A complete account of the arrangement of its component parts would necessitate very full and minute descriptions, which could only be elucidated by numerous illustrative figures.

The lens is situated behind the pupil, in what is called the hyaloid fossa of the vitreous humor, which is exactly moulded to its posterior convexity. In the fœtus, the capsule of the lens receives a branch from the arteria centralis, but it is non-vascular in the adult. The anterior convexity of the lens is just behind the iris, and its borders are in relation with what is known as the suspensory ligament. The convexities do not present regular curves, and they are so subject to variations after death that the measurements, post-mortem, are of little value. During life, however, they have been measured very exactly in the various conditions of accommodation. These measurements will be discussed fully in connection with the physiology of the lens.

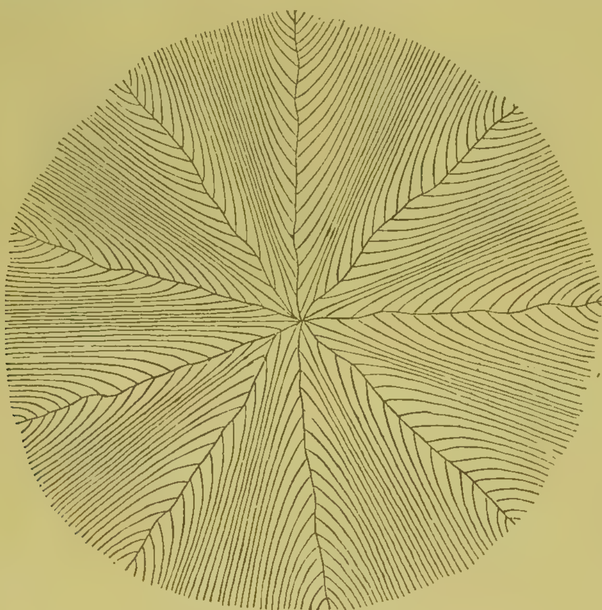


FIG. 246.—*Crystalline lens, anterior view.* (Babuchin.)

The diameters of the lens in the adult are about $\frac{1}{3}$ of an inch transversely and $\frac{1}{4}$ of an inch antero-posteriorly. The convexity is greater on its posterior than on its anterior surface. In fœtal life, the convexities of the lens are much greater than in the adult and its structure is much softer. In old age, the convexities are diminished and the lens becomes harder and quite inelastic, which accounts for the progressive diminution in the power of accommodation.

The important physiological points in the structure of the lens are that it presents an investing membrane, the capsule, the lens itself being composed of layers of fibres of different degrees of density.

The capsule of the lens is an exceedingly thin, transparent membrane, very elastic, so that, when it is torn, the force of its contraction frequently expels its contents. This membrane is generally from $\frac{1}{2400}$ to $\frac{1}{1500}$ of an inch thick; but it is very thin at the periphery, measuring here only $\frac{1}{6000}$ of an inch. Its thickness is increased in old age. On the anterior portion, the capsule is lined with a layer of exceedingly delicate, nucleated epithelial cells. These are situated on the inner surface of the membrane. The posterior half of the capsule has no epithelial lining. The cells are regularly polygonal, measuring from $\frac{1}{2500}$ to $\frac{1}{1200}$ of an inch in diameter, with large, round nuclei. After death they are said to break down into a liquid, known as the liquid of Morgagni, though by some this liquid is supposed to be exuded from the substance of the lens. At all events, the cells disappear soon after death.

If the lens be viewed entire with a low magnifying power, it presents, upon either of its surfaces, a star with from nine to sixteen radiations extending from the centre to

FIG. 247.—*Crystalline lens, posterior view.* (Babuchin.)

about half or two-thirds of the distance to the periphery. The stars seen upon the two surfaces are not coincident, the rays of one being situated between the rays of the other. In the fœtus, the stars are more simple, presenting only three radiations upon either surface. These stars are not fibrous, like the rest of the lens, but are composed of a homogeneous substance, which extends, also, between the fibres.

The greatest part of the substance of the lens is composed of very delicate, soft, and pliable fibres, which are transparent, but perfectly distinct. These fibres are flattened, six-sided prisms, closely packed together, so that their transverse section presents a regularly-tesselated appearance. They are from $\frac{1}{4800}$ to $\frac{1}{2400}$ of an inch broad and from $\frac{1}{13000}$ to $\frac{1}{9000}$ of an inch in thickness. Their flat surfaces are parallel with the surface of the lens. The direction of the fibres is from the centre and from the rays of the stellate figures to the periphery, where they turn and pass to the star upon the opposite side. The outer layers of fibres, near the equator, or circumference of the lens, are provided with exceedingly distinct, oval nuclei, with one or two nucleoli. These become smaller as we pass deeper into the substance of the lens, and gradually they disappear.

The regular arrangement of the fibres of the lens makes it possible to separate its substance into laminæ, which have been compared by anatomists to the layers of an onion; but this separation is entirely artificial, and the number of apparent layers depends upon the dexterity of the manipulator. It is to be noted, however, that the external portions of the lens are soft, even gelatinous, and that the central layers are much harder, forming a sort of central kernel, or nucleus.

The lens is composed of a peculiar organic nitrogenized substance, very analogous to globuline, called crystalline, combined with various inorganic salts. One of the peculiar constituents of this body is cholesterine. In an examination of four fresh crystalline lenses of the ox, we found cholesterine, in the proportion of 0·907 of a part per 1,000. In some cases of cataract, cholesterine exists in the lens in a crystalline form; but, under normal conditions, it is united with the other constituents.

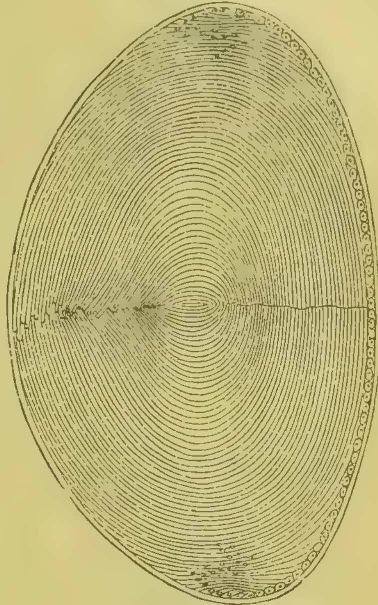


Fig. 248.—*Section of the crystalline lens.* (Babuchin.)

Suspensory Ligament of the Lens (Zone of Zinn).—When we come to the description of the vitreous humor, we shall see that it occupies about the posterior two-thirds of the globe, and is enveloped in a delicate capsule, called the hyaloid membrane. In the region of the ora serrata of the retina, this membrane divides into two layers. The posterior layer lines the depression in the vitreous humor into which the lens is received. The anterior layer passes forward toward the lens and divides into two secondary layers, one of which passes forward to become continuous with the anterior portion of the capsule of the lens, while the other passes to the posterior surface of the lens to become continuous with this portion of its capsule. The anterior of these layers is corrugated, or thrown into folds which correspond with the ciliary processes, with which it is in contact. This corrugated portion is called the zone of Zinn. The two layers thus surround the lens and are properly called its suspensory ligament. As the two layers of the suspensory ligament separate at a certain distance from the lens, one passing to the anterior and the other to the posterior portion of the capsule, there remains a triangular canal, about $\frac{1}{10}$ of an inch wide, surrounding the border of the lens, called the canal of Petit. Under natural conditions, the walls of this canal are nearly in apposition and it contains a very small quantity of clear liquid.

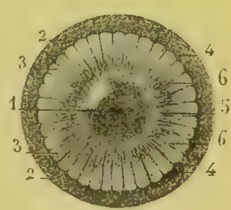


Fig. 249.—*Zone of Zinn.* (Sappey.)

1, crystalline lens; 2, 2, vitreous humor; 3, 3, zone of Zinn; 4, 4, posterior portion of the zone of Zinn, thrown into folds; 5, 6, 6, anterior and middle portions of the zone of Zinn.

As we have already remarked in describing the retina, at the ora serrata, the membrane is closely connected, by a mutual interlacement of fibres, with the suspensory ligament. It is important to appreciate clearly the relations of the suspensory ligament, in order to understand the mechanism of accommodation of the lens to vision at different distances. The ciliary muscle being in repose, during what is termed the indolent condition of the eye, when it is adapted to vision at long distances, the tension of the parts flattens the lens; but, in the effort of accommodation for near objects, the ciliary muscle contracts, compresses the contents of the globe, relaxes the suspensory ligament, and the inherent elasticity of the lens renders it more convex. It is by a delicate use of this muscle, that the proper adaptation of the curvatures of the lens is obtained.

The membrane forming the suspensory ligament is composed of pale longitudinal and transverse fibres of rather a peculiar appearance, which are much less affected by acetic acid than the ordinary fibres of connective tissue.

Aqueous Humor.—The space bounded in front by the cornea, posteriorly by the crystalline lens and the anterior face of its suspensory ligament, and, at its circumference, by the tips of the ciliary processes, is known as the aqueous chamber. This contains a clear liquid, called the aqueous humor. The iris separates this space into two divisions, which communicate with each other through the pupil; viz., the anterior chamber, situated between the anterior face of the iris and the cornea, and the posterior chamber, between the posterior face of the iris and the crystalline. It is evident, from the position of the iris, that the anterior chamber is much the larger; and, indeed, the posterior surface of the iris and the anterior surface of the lens are in contact, except, perhaps, near their periphery or when the iris is very much dilated. The liquid filling the chambers of the eye is said to be secreted by the blood-vessels of the ciliary processes; at all events, it is rapidly reproduced after it has been evacuated, as occurs in many surgical operations upon the eye.

There is very little to be said concerning the properties and composition of the aqueous humor. It is perfectly colorless and transparent, faintly alkaline, of a specific gravity of about 1005, and possesses the same index of refraction as the cornea and the vitreous humor. As we should infer from its low specific gravity, the aqueous humor is composed chiefly of water. It contains a small quantity of an albuminoid matter, but it is not rendered turbid by heat or other agents which coagulate albumen. Various inorganic salts (the chlorides, sulphates, phosphates, and carbonates) exist in this liquid, in small proportion. It contains also traces of urea and glucose.

Vitreous Humor.—The vitreous humor is a clear, glassy substance, occupying about the posterior two-thirds of the globe. It is enveloped in an exceedingly delicate, structureless capsule, called the hyaloid membrane, which is about $\frac{1}{7000}$ of an inch in thickness. This membrane adheres pretty strongly to the limitary membrane of the retina. In front, at the ora serrata, as we have already seen, the hyaloid membrane is thickened and becomes continuous with the suspensory ligament of the lens.

The vitreous humor itself is gelatinous, of feeble consistence, slightly alkaline in its reaction, with a specific gravity of about 1005. Upon section, there oozes from it a watery fluid of a slightly mucilaginous consistence. This humor is not affected by heat or alcohol, but it is coagulated by certain mineral salts, more especially the acetate of lead. When thus solidified, it presents regular layers, like the white of an egg boiled in its shell; but these are artificial. In the embryon, the vitreous humor is divided into numerous little cavities and contains cells and leucocytes. It is also penetrated by a branch from the central artery of the retina, which passes through its centre to ramify on the posterior surface of the crystalline lens. This structure, however, is not found in the adult, the vitreous humor being then entirely without blood-vessels.

There is still considerable difference of opinion with regard to the structure of the vitreous humor in the adult, some anatomists believing that it is perfectly homogeneous and that the so-called laminæ are produced only by the action of reagents, while others state that it is divided into compartments, by processes penetrating from and connected with the hyaloid membrane. The weight of authority is decidedly in favor of a subdivision of the humor into compartments formed by delicate membranes radiating from the point of penetration of the optic nerve to the anterior boundary where the hyaloid membrane is in contact with the capsule of the lens. In this way, the humor is divided up, something like the half of an orange, by about one hundred and eighty membranous processes of extreme delicacy, which do not interfere with its transparency.

Summary of the Anatomy of the Globe of the Eye.

For the intimate structure of the various coats of the eye, their dimensions, etc., the reader is referred to the descriptions just given of these parts. In this summary, we propose simply to show the relations of the various parts, giving at the same time a brief statement of their physiological importance. This end will be attained by a full explanation of Fig. 250, which represents a section of the human eye and shows the relations of its various coats, humors, etc.

The eyeball is nearly spherical in its posterior five-sixths, its anterior sixth being formed of the segment of a smaller sphere, which is slightly projecting. In its posterior five-sixths, it presents the following coats, indicated in the figure:

S. The sclerotic; a dense, fibrous membrane, chiefly for the protection of the more delicate structures of the globe, and giving attachment to the muscles which move the eyeball. Attached to the sclerotic, are the tendons of R, R, the recti muscles.

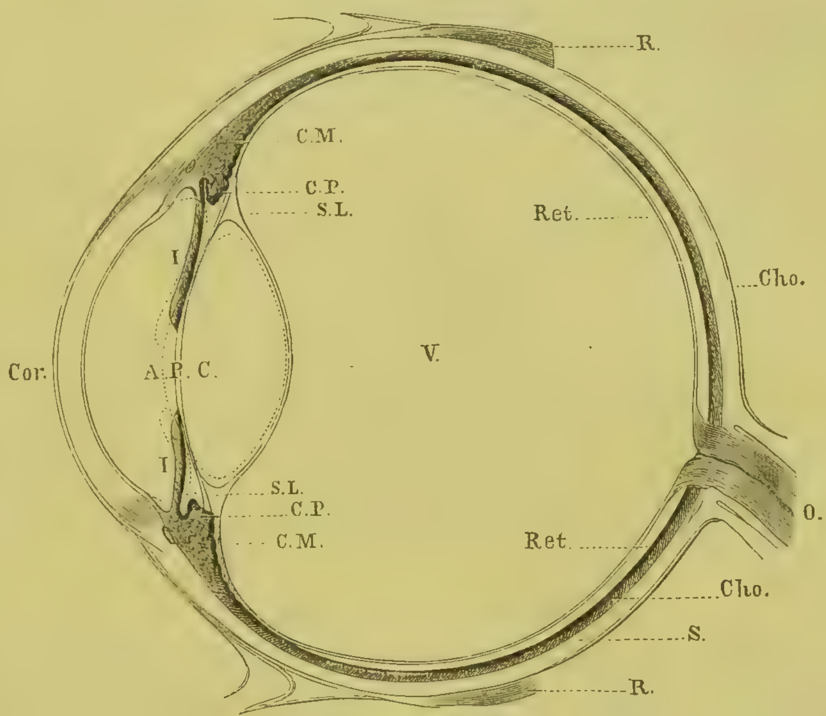


FIG. 250.—*Section of the human eye, copied from Helmholtz and slightly modified.*

Cor. The cornea; a transparent structure, forming the anterior, projecting sixth of the globe; dense and resisting, allowing, however, the passage of light; covered, on its convex surface, with several layers of transparent epithelial cells, and, on its posterior surface, with the membrane of the aqueous humor.

Cho. The choroid coat, lining the sclerotic and extending only as far forward as the cornea; connected with the sclerotic by loose connective tissue, in which ramify blood-vessels and nerves, and presenting an external, vascular layer and an internal, pigmentary layer, which latter gives its characteristic dark-brown color.

C. P., C. P. The ciliary processes; peculiar folds of the choroid, which form its anterior border, and which embrace the folds of the suspensory ligament of the lens.

C. M., C. M. The ciliary muscle, formerly called the ciliary ligament; a muscular ring, situated just outside of the ciliary processes, arising from the circular line of junction of the sclerotic with the cornea, and passing over the ciliary processes, to become lost in the fibrous tissue of the choroid. This is sometimes called the tensor of the choroid. Its action is to tighten the choroid over the vitreous humor and to relax the ciliary processes and the suspensory ligament of the lens, when the lens, by virtue of its elasticity, becomes more convex. The ciliary muscle is the active agent in accommodation. In the figure, the mechanism of accommodation is shown by the dotted lines, which represent the suspensory ligament relaxed by the contraction of the ciliary muscle, and the lens, increased in its convexity, pushing forward the iris.

I., I. The iris; dividing the space in front of the lens into two chambers occupied by the aqueous humor: (A) The anterior chamber is much the larger. The iris, in its central portion surrounding the pupil (P), is in contact with the lens. Its circumference is just in front of the line of origin of the ciliary muscle.

Ret., Ret. The retina; an exceedingly delicate, transparent membrane, lining the choroid and extending to about $\frac{1}{15}$ of an inch behind the ciliary processes, the anterior margin forming the ora serrata. O. The optic nerve penetrating the retina a little internal to and below the antero-posterior axis. The layer of rods and cones is situated externally, next the choroid. Internal to the layer of rods and cones, are the four granular layers; next, the layer of nerve-cells; next, the expansion of the fibres of the optic nerve; and next, in apposition with the hyaloid membrane of the vitreous humor, is the limitary membrane. The layer of rods and cones is supposed to be the portion which receives visual impressions, the rods and cones being connected with the nerve-cells, and through them with the fibres of the optic nerve, by delicate filaments. The macula lutea and the fovea centralis are exactly in the axis of distinct vision.

C. The crystalline lens; elastic, transparent, enveloped in its capsule and surrounded by S. L., S. L., the suspensory ligament.

S. L., S. L. The suspensory ligament; the anterior layer connected with the anterior portion of the capsule of the lens, and the posterior, with the posterior portion of the capsule. The folded portion of this ligament, which is received between the folds of the ciliary processes, is called the zone of Zinn. The triangular canal between the anterior and the posterior layers of the suspensory ligament and surrounding the equator of the lens is called the canal of Petit.

V. The vitreous humor; enveloped in the structureless hyaloid membrane, which membrane is continuous in front with the suspensory ligament of the lens.

Refraction in the Eye.

It is simply impossible to obtain a clear idea of the physiology of vision without having carefully studied the physiological anatomy of the visual organs; and, for this reason, we have been as exact as possible and somewhat minute in our description of the structure of the eye. If the student will carefully study the anatomy of the parts, a very succinct statement of some of the well-established laws of refraction will render the physiology so simple that it will follow almost without explanation.

In applying the laws of the refraction of light to the transparent media of the eye, it is necessary to bear in mind certain general facts with regard to vision, that have as yet been referred to either very briefly or not at all.

The eye is not by any means a perfect optical instrument, looking at it from a purely physical point of view. This statement, however, should not be understood as implying that the arrangement of the organs of vision is not such as to adapt them perfectly to the functions which they have to perform in connection with the proper appreciation of visual impressions. By physical tests, it can be demonstrated that the eye is not entirely achromatic; but, in ordinary vision, the dispersion of colors is not appreciated. There is but a single point in the retina, the fovea centralis, where vision is absolutely distinct; and it is upon this point that images are made to fall when the eye is directed toward any particular object.

It is curious to note, however, that the refracting apparatus is not exactly centred, a condition so essential to the satisfactory performance of our most perfect optical instruments. For example, in a compound microscope or a telescope, the centres of the different lenses entering into the construction of the instrument are all situated in a straight line. Were the eye a perfect optical instrument, the line of vision would coincide exactly with the axis of the cornea; but this is not the case. The visual line (a line drawn from an object to its image on the fovea centralis) deviates from the axis of the cornea, in normal eyes, to the nasal side. The visual line, therefore, forms an angle with the axis of the cornea. This is known as the angle alpha. This deviation of the visual line from the mathematical centre of the eye is observed both in the horizontal and in the vertical planes. "The horizontal deviation varies from two to eight degrees (*Schuerman*), the vertical, from one to three degrees (*Mandelstamm*)." Of course, this want of exact centration of the optical apparatus, in normal eyes, does not practically affect distinct vision, for, when the eyes are directed toward any object, this object is brought in the line of the visual axis; but the angle alpha is an important element to be taken into account in various mathematical calculations connected with the physics of the eye.

The field, or area of distinct vision, is quite restricted; but, were it larger, it is probable that the mind would become confused with the extent and variety of the impressions, and that we should be unable so easily to observe minute details and fix the attention upon small objects.

While we see certain objects with absolute distinctness in a restricted field, the angle of vision is very wide, and rays of light are admitted from an area equal nearly to the half of a sphere. Such a provision is eminently well adapted to our requirements. We direct the eyes to a particular point and see a certain object distinctly, getting the advantage of an image in the two eyes exactly at the points of distinct vision; the rays coming from without the area of distinct vision are received upon different portions of the surface of the retina and produce an impression more or less indistinct, not interfering with the observation of the particular object to which the attention is for the moment directed; but, even while looking intently at any object, the attention may be attracted by another object of an unusual character, which might, for example, convey an idea of danger, and the point of distinct vision can be turned in its direction. Thus, while we see distinctly but few objects at one time, the area of indistinct vision is immense; and our attention may be readily directed to unexpected or unusual objects that may come within any portion of the field of view. The small extent of the area of distinct vision, especially for near objects, may be readily appreciated if we watch a person attentively reading a book, when the eyes will be seen to follow the lines from one side of the page to the other with perfect regularity. When we consider that, in addition to these remarkable qualities, which are never thought of in artificial optical instruments, the eye may be accommodated at will, with the most exquisite nicety, to vision at different distances, and that we possess correct appreciation of form, etc., by the use of the two eyes, it is evident that the organ of vision gains rather than loses in comparison with the most perfect instruments that have ever been or probably ever will be constructed.

Laws of Refraction, Dispersion, etc., bearing upon the Physiology of Vision.—In the present state of physiological science, we have little to do with the theory of light, except as regards the modifications of luminous rays in passing through the refracting media of the eye. It will be sufficient to state that nearly all physicists of the present day agree in accepting what is known as the theory of undulation, rejecting *in toto* the emission-theory proposed by Newton. It is necessary to the theory of undulation to assume that all space and all transparent bodies are permeated with what has been called a luminiferous ether; and that light is propagated by a vibration or an undulation of this hypothetical substance. This theory assimilates light to sound, in the mechanism of its propagation; but, in sound, the waves are supposed to be longitudinal, or to follow the line of propagation, while in light the particles are supposed to vibrate transversely, or at right angles to the line of propagation. It must be remembered, however, that the undulatory theory of sound is capable of positive demonstration, and that the propagation of sound by waves can only take place through ponderable matter, the vibrations of which can always be observed; while luminous vibrations involve the existence of an impónderable and a purely hypothetical ether. It is possible, indeed, that scientific facts may, in the future, render the existence of such an ether improbable or its supposition unnecessary; but, at present, all we can say is that the theory of luminous undulation is entirely in accord with the optical phenomena that have thus far been recognized.

The different calculations of physicists with regard to the velocity of light have been remarkably uniform in their results. The lowest calculations put it at about 185,000 miles in a second, and the highest, at about 195,000 miles. The rate of propagation is usually assumed to be about 192,000 miles.

The intensity of light is in proportion to the amplitude of the vibrations. The intensity diminishes as the distance of the luminous body increases, and is in inverse ratio to the square of the distance.

In the theory of the colors into which pure white light may be decomposed by prisms, it is assumed, as a matter of demonstration, that the waves of the different colors of the solar spectrum are not of the same length. The decomposition of light is produced by differences in the refrangibility of the different colored rays as they pass through a denser medium than the air. The differences in the wave-lengths for different colors is very simply set forth by Tyndall as follows:

"The color of light is determined solely by its wave-length. The ether-waves gradually diminish in length from the red to the violet. The length of a wave of red light is about $\frac{1}{39000}$ of an inch; that of the wave of violet light is about $\frac{1}{57500}$ of an inch. The waves which produce the other colors of the spectrum lie between these extremes.

"The velocity of light being 192,000 miles in a second, if we multiply this number by 39,000, we obtain the number of waves of red light in 192,000 miles; the product is 474,439,680,000,000. All of these waves enter the eye in a second. In the same interval 699,000,000,000,000 waves of violet light enter the eye. At this prodigious rate is the retina hit by the waves of light.

"Color, in fact, is to light, what pitch is to sound. The pitch of a note depends solely on the number of aërial waves which strike the ear in a second. The color of light depends on the number of ethereal waves which strike the eye in a second. Thus the sensation of red is produced by imparting to the optic nerve four hundred and seventy-four millions of millions of impulses per second, while the sensation of violet is produced by imparting to the nerve six hundred and ninety-nine millions of millions per second." In this way the scale of colors in the solar spectrum is compared to the scale of musical notes and intervals. Indeed, Helmholtz has constructed a theoretical scale of colors to correspond with musical tones and semitones.

The analysis of white light into the different colors of the spectrum shows that it is compound; and, by synthesis, the colored rays may be brought together, producing white light. Colors may be obtained by decomposition of light by transparent bodies, the different colored rays being refracted, or bent by a prism at different angles. It is not in this way, however, that the colors of different objects are produced. Certain objects have the property of reflecting the rays of light. A perfectly smooth, polished surface, like a mirror, may reflect all of the rays; and the object then has no color, the reflected light only being appreciated by the eye. Certain other objects do not reflect all of the rays of light, some of them being lost to view or absorbed. When an object absorbs all of the rays, it has no color and is called black. When an object absorbs the rays equally and reflects a portion of these rays without decomposition, it is gray or white. There are many objects, however, that decompose white light, absorbing certain rays of the spectrum and reflecting others. The rays not absorbed, but returned to the eye by reflection, give color to the object. Thus, if an object absorb all of the rays of the spectrum except the red, the red rays strike the eye, and the color of the object is red. So it is with objects of different shades, the colors of which are given simply by the unabsorbed rays.

It is a curious fact that the mixture of different colors in certain proportions will result in white. Two colors, which, when mixed, result in white, are called complementary. The following colors of the spectrum bear such a relation to each other:

Red and greenish-blue.
Orange and cyanogen-blue.
Yellow and indigo-blue.
Greenish-yellow and violet.

The fact that impressions made upon the retina persist for an appreciable length of time enables us to illustrate the law of complementary colors. If a disk, presenting divisions with two complementary colors, be made to revolve so rapidly that the impressions made by the two colors are blended, the resulting color is white.

It is almost useless, with our present knowledge, to speculate with regard to the probable mechanism of the appreciation of colors in vision. The facts just stated are sufficiently clear, showing that the number of ethereal vibrations is different for different colors; but it is by no means determined that differences in the amplitude of the vibrations are in direct relation with the arrangement of the disks of the rods and cones in different portions of the retina, a theory lately proposed by Zenker. The curious phenomena of color-blindness depend upon an abnormal condition of the visual apparatus. Persons possessing this peculiarity—called sometimes Daltonism, after the celebrated English chemist, who described this infirmity as it existed in his own person—although vision may be normal in other respects, cannot distinguish certain colors, will mistake red for green, etc., and some can only distinguish black and white. It is a curious fact, also, that persons affected with color-blindness (Daltonism, or achromatopsia) are sometimes incapable of distinguishing different musical tones. Although often congenital and irremediable, it is now known that color-blindness is sometimes produced by the excessive use of alcohol and tobacco, exposure to cold and wet, etc., and is amenable to treatment.

Refraction by Lenses.—A ray of light is an imaginary pencil, so small as to present but a single line; and the light admitted to the interior of the eye by the pupil is supposed to consist of an infinite number of such rays. In studying the physiology of vision, it is important to recognize the laws of refraction of rays by transparent bodies bounded by curved surfaces, with particular reference to the action of the crystalline lens.

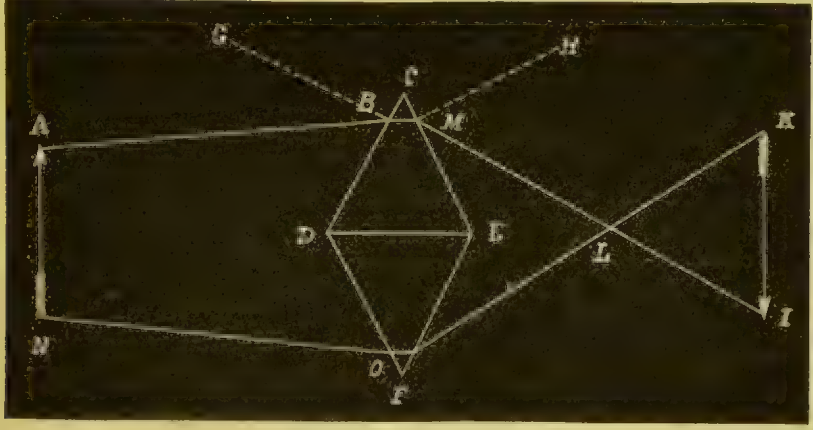


FIG. 251.—*Refraction by prisms.*

The action of a double-convex lens, like the crystalline, in the refraction of light, may be readily understood if we simply apply the well-known laws of refraction by prisms. A ray of light falling upon the side of a prism at an angle is deviated toward a line perpendicular to the surface of the prism. As the ray passes from the prism to the air, it is again refracted, but then the deviation is from the perpendicular of the second surface of the prism. If we imagine two prisms placed together, as in Fig. 251, the ray A B will be bent toward the perpendicular G B to M. As it passes from the prism, it will be refracted from the perpendicular H M and take the direction M L. Corresponding refraction takes place in the ray N O falling upon the lower prism. These two rays will cross each other at the point L.

A circle is supposed to be equivalent to a polygon with an infinite number of sides. A regular double-convex lens is a transparent body bounded by portions of a sphere, and it may be assumed to be composed of an infinite number of prisms. The action of a convex lens is to converge the rays of light falling upon different portions of their surface so that they cross at a certain distance behind the lens. If we imagine the lens A B (Fig. 252) to be free from spherical aberration, the rays C D and C E, from the point C, will

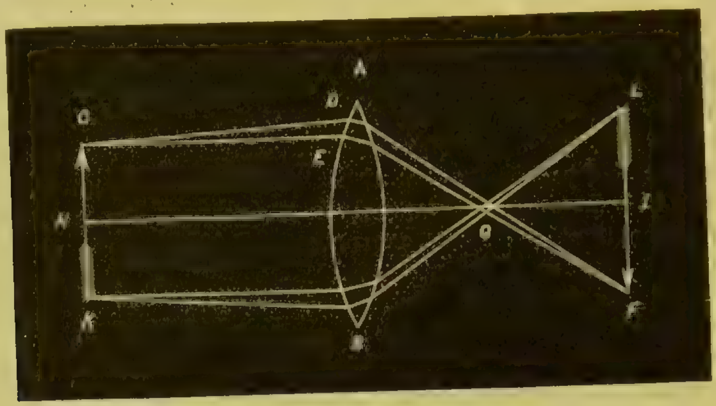


FIG. 252.—*Refraction by convex lenses.*

be refracted and brought to a focus at the point F. In the same way, the rays from the point K will be brought to a focus at the point L, the two sets of rays crossing at G. The same is true for all the rays from the object C K, which strike the lens at an angle; but the ray H I, which is perpendicular to the lens, is not deviated. The line H I is called the axis of the lens. These facts may be applied to the crystalline lens. The rays from an object C K fall upon the lens and are brought to a focus so as to produce the image L F. The retina is supposed to be at such a distance from the lens that the rays are brought to a focus exactly at its surface. Inasmuch as the rays cross each other at the point G, the image is always inverted.

Supposing the crystalline lens to be free from spherical and chromatic aberration, the formation of a perfect image depends upon the following conditions:

The object must be at a certain distance from the lens. If the object be too near, the rays, as they strike the lens, are too divergent and are brought to a focus beyond the plane L I F, or behind the retina; and, as a consequence, the image is confused. In optical instruments, the adjustment is made for objects at different distances by moving the lens itself. In the eye, however, the adjustment is effected by increasing or diminishing the curvatures of the lens, so that the rays are always brought to a focus at the visual surface of the retina. The faculty of thus changing the curvatures of the crystalline lens is called accommodation. This power, however, is restricted within certain well-defined limits.

In some individuals, the antero-posterior diameter of the eye is too long, and the rays, for most objects, come to a focus before they reach the retina. This defect may be remedied by placing the object very near the eye, so as to increase the divergence of the rays as they strike the crystalline. Such persons are said to be near-sighted (myopic), and objects are seen distinctly only when very near the eye. This defect may be remedied for distant objects by placing concave lenses before the eyes, by which the rays falling upon the crystalline are diverged. The opposite condition, in which the antero-posterior diameter is too short (hypermetropia), is such that the rays are brought to a focus behind the retina. This is corrected by converging the rays of incidence by placing convex lenses before the eyes. In old age, the crystalline lens becomes flattened, its elasticity is diminished, and the power of accommodation is lessened; conditions which also tend to bring the rays to a focus behind the retina. This condition is called presbyopia. To render near vision, as in reading, distinct, objects are placed farther from the eye than under normal conditions. The defect may be remedied, as in hypermetropia, by placing convex lenses before the eyes, by which the rays are converged before they fall upon the crystalline lens.

The mechanism of accommodation will be fully considered in connection with the physiology of the crystalline lens; and at present, it is sufficient to state that, in looking at distant objects, the rays, as they fall upon the lens, are nearly parallel. The lens is then in repose, or "indolent." It is only when an effort is made to see near objects distinctly, that the agents of accommodation are called into action; and then, very slight changes in the curvature of the lens are sufficient to bring the rays to a focus exactly on the visual surface of the retina.

Spherical Aberration.—In a convex lens, with its surfaces consisting of portions of a perfect sphere, the rays of light from any object are not converged to a uniform focus, and the production of an absolutely distinct image is impossible. For example, if we suppose the crystalline lens to present regular curvatures, the rays refracted by its peripheral portion would be brought to a focus in front of the retina; the focus of the rays converged by the lens near its centre would be behind the retina; a few, only, of the rays would have their focus at the retina itself; and, as a consequence, the image would appear confused. This is illustrated in imperfectly-corrected lenses and is called spherical aberration. For example, in examining an object with an imperfectly-corrected objective under the microscope, it is evident that the field of view is not uniform, and that there is a different focal adjustment for the central and the peripheral portions of the lens. In the construction of optical instruments, this difficulty may be in part corrected if the rays of light be cut off from the periphery of the lens by a diaphragm, which is an opaque screen with a circular perforation allowing the rays to pass to a restricted portion of the lens near its centre. The iris corresponds to the diaphragm of optical instruments, and it corrects the spherical aberration of the crystalline in part, by eliminating a portion of the rays that would otherwise fall upon its peripheral portion. But this correction is not sufficient for high magnifying powers; and it is only by the more or less perfect correction of this kind of aberration by other means, that powerful lenses have been rendered available in optics.

The spherical aberration of lenses which diverge the rays of light is precisely opposite to the aberration of converging lenses. If, therefore, we construct a compound lens, it is possible to fulfil the conditions necessary to the convergence of all the incident rays to a focus on a uniform plane, so that the image produced behind the lens is not distorted. Given, for example, a double-convex lens, by which the rays are brought to innumerable focal points situated in different planes. The fact that but a few of these focal points are in the plane of the retina renders the image indistinct. If we place behind this convex lens a concave lens, by the action of which the rays are more or less diverged, the inequality of the divergence by different portions of the second lens will have the following effect: As the angle of divergence gradually increases from the centre toward the periphery, the rays near the periphery, which are most powerfully converged by the convex lens, will be most widely diverged by the peripheral portion of the concave lens; so that, if the opposite curvatures be accurately adjusted, the aberrant rays may be blended. It is evident that, if all of the rays were equally converged by the convex lens and equally diverged by the concave lens, the action of the latter would be simply to elongate the focal distance; and it is equally evident that, if the aberration of the one be exactly opposite to the aberration of the other, there will be perfect correction. Mechanical art has not enabled us to effect correction of every portion of very powerful convex lenses in this way; but, by a combination of lenses and diaphragms together, highly-magnified images, nearly perfect, have been produced.

It is evident that, for distinct vision at different distances, the crystalline lens must be nearly free from spherical aberration. This is not effected by a combination of lenses, as in ordinary optical instruments, but by the curvatures of the lens itself, and by certain differences in the consistence of different portions of the lens, which will be fully considered hereafter.

Chromatic Aberration.—We have already alluded to the fact that a refracting medium does not act equally upon the different colored rays into which pure white light may be decomposed; in other words, as the pure ray falling upon the inclined surface of a glass prism is bent, it is decomposed into the colors of the spectrum. As a convex lens is practically composed of an infinite number of prisms, the same effect would be expected. Indeed, a simple convex lens, even if the spherical aberration be corrected, always produces more or less decomposition of light. The image formed by such a lens will consequently be colored; and this defect in simple lenses is called chromatic aberration. At the same time, it is evident that the centre of the different rays from an object will be composed of all the colors of the spectrum combined, producing the effect of white light; but, at the borders, the different colors will be separate and distinct, and an image produced by a simple convex lens will thus be surrounded by a circle of colors like a rainbow.

In prisms, the chromatic dispersion may be corrected by allowing the colored rays from one prism to fall upon a second prism, which is inverted, so that the colors will be brought together and produce white light. Two prisms thus applied to each other constitute, in fact, a flat plate of glass, and the rays of light pass without deviation. If this law be applied to lenses, it is evident that the dispersive power of a convex lens may be exactly opposite to that of a concave lens. By the convex lens, the colored rays are separated by convergence and cross each other; while, in the concave lens, the colored rays are dispersed in the opposite direction. If, then, we combine a convex with a concave lens, the white light decomposed by the one will be recomposed by the other, and the chromatic aberration will thus be corrected. But, in using a convex and a concave lens composed of the same material, the convergence by the one will be neutralized by the dispersion of the other, and there will be no amplification of the object.

In the construction of optical instruments, the chromatic aberration is corrected, with but slight diminution in the amplification, by combining lenses made of different material, as of flint-glass and crown-glass. Flint-glass has a much greater dispersive power than crown-glass. If, therefore, we use a convex lens of crown-glass combined with a concave lens of flint-glass, the chromatic aberration of the convex lens may be corrected by a concave lens with a curvature which will take but little from the magnifying power. A compound lens, with the spherical aberration of the convex element corrected by the curvature of a concave lens, and the chromatic aberration corrected by the curvature, in part, and in part by the superior refractive power of flint-glass over crown-glass, will produce a perfect image.

Although the eye is not absolutely achromatic, the dispersion of light is not sufficient to interfere with distinct vision. We can understand how the chromatic aberration is practically corrected in the crystalline lens, when we remember that its various layers are of different consistence and of different refractive power.

Formation of Images in the Eye.

It is only necessary to call to mind the general arrangement of the different structures in the eye and to apply the simple laws of refraction, to comprehend precisely how images are formed upon the retina.

The eye corresponds to a camera obscura. Its interior is lined with a dark, pigmentary membrane (the choroid), the function of which is to prevent the confusion of images by internal reflection. The rays of light are admitted through a circular opening (the pupil), the size of which is regulated by the movements of the iris. The pupil is contracted when the light striking the eye is intense and is dilated as the amount of light is diminished. In the accommodation of the eye, the pupil is dilated for distant objects and contracted for near objects; for, in looking at near objects, the aberrations of sphericity and achromatism in the lens are more marked, and the peripheral portion is cut off by the action of this movable diaphragm, thus aiding the correction. The rays of light from an object pass through the cornea, the aqueous humor, the crystalline lens, and the vitreous humor, and they are refracted with so little spherical and chromatic aberration, that the image formed upon the retina is practically perfect. The layer of rods and cones of the retina is the only portion of the eye endowed directly with special sensibility, the impressions of light being conveyed to the brain by the optic nerves. This layer is situated next the choroid, but the other layers of the retina, through which the light passes to reach the rods and cones, are perfectly transparent.

It has been positively demonstrated that the rods and cones are the only structures capable of directly receiving visual impressions, by the following interesting experiment, first made by Purkinje: We concentrate upon the sclerotic, with a convex lens of short focus, an intense light, at a point as far as possible removed from the cornea. This passes through the translucent coverings of the eye at this point, and the image of the light reaches the retina. If we then look at a dark surface, we have the field of vision presenting a reddish-yellow illumination, with a dark, arborescent appearance produced by the shadow of the large retinal vessels; and, as we move the lens slightly, the shadow of the vessels moves with it. Without going elaborately into the mechanism of this remarkable phenomenon, it is sufficient to state that Heinrich Müller has arrived at an absolute mathematical demonstration that the shadows of the vessels are formed upon the layer of rods and cones, and that this layer alone is capable of receiving impressions of light. His explanation is accepted by all writers at the present day and is regarded as positive proof of the peculiar sensibility of this portion of the retina. In carefully-conducted observations of this kind, a spot is seen in which no vessels appear, which corresponds to the fovea centralis. When the experiment is prolonged, the vessels disappear, as the sensibility of the retina becomes diminished by fatigue.

Theoretically, an illuminated object placed in the angle of vision would form upon the retina an image, diminished in size and inverted. This fact is capable of actual demonstration by means of the ophthalmoscope. With this instrument, the retina and the images formed upon it may be seen during life with perfect distinctness.

All parts of the retina, except the point of entrance of the optic nerve, are sensitive to light; and the arrangement of the cornea and pupil is such, that the field of vision is, at the least estimate, equal to the half of a sphere. If a ray of light fall upon the border of the cornea at a right angle to the axis of the eye, it is refracted by its surface and will pass through the pupil to the border of the retina upon the opposite side. Above and below, the circle of vision is cut off by the overhanging arch of the orbit and the malar prominence; but externally the field is free. With the two eyes, therefore, the lateral field of vision must be equal to at least one hundred and eighty degrees. It is easy to demonstrate, however, by the ophthalmoscope, as well as by taking cognizance of the impressions made by objects far removed from the axis of distinct vision, that images formed upon the lateral and peripheral portions of the retina are confused and imperfect.

We have a knowledge of the presence and an indefinite idea of the general form of large objects situated outside of the area of distinct vision; but, when we wish to note such objects exactly, the eyeball is turned by muscular effort, so as to bring them at or very near the axis of the globe. This fact, with what we know of the mechanism of refraction by the cornea and lens, makes it evident that the area of the retina upon which images are formed with perfect distinctness is quite restricted. A moment's reflection is sufficient to convince any one that, in order to see any object distinctly, we must look at it, or bring the axis of the eye to bear upon it directly. Let us see, now, how far this fact is capable of positive demonstration.

If we examine the bottom of the eye with the ophthalmoscope, we can see the yellow spot with the fovea centralis, apparently free from blood-vessels, and composed, as we know, chiefly of those elements of the retina which are sensitive to light. If, at the same time, we examine an image for which the eye is perfectly adjusted, it will be seen that this image is perfect only at the fovea centralis; and, if the object be removed from the axis of vision, we see a confused image upon the retina removed from the fovea, at the same time that the subject is conscious of indistinct vision. In the words of Helmholtz, "It is only in the immediate vicinity of the ocular axis that the retinal image possesses entire distinctness; beyond this, the contours are less defined. It is in part for this reason that in general we see distinctly in the field of vision, only the point that we fix. All the others are seen vaguely. This lack of distinctness in indirect vision, in addition, depends also upon diminished sensibility of the retina: at a slight distance from the fixed point, the distinctness of vision has diminished much more than the objective distinctness of retinal images."

At the point of penetration of the optic nerve, the retina is insensible to luminous impressions; at least, its sensibility is here so obtuse as to be entirely inadequate for the purposes of vision. This point is called the punctum cæcum; and its want of sensibility was demonstrated many years ago (1668) by Mariotte. The classical experiment by which this important fact was positively ascertained, which is generally known to physiologists as Mariotte's experiment, is so curious that we quote it *verbatim*:

"I fasten'd on an obscure Wall about the hight of my Eye, a small round paper, to serve me for a fixed point of Vision; and I fastened such an other on the side thereof towards my right hand, at the distance of about 2. foot; but somewhat lower than the first, to the end that it might strike the *Optick Nerve* of my Right Eye, whilst I kept my Left shut. Then I plac'd myself over against the First paper, and drew back by little and little, keeping my Right Eye fixt and very steddy upon the same; and being about 10. foot distant, the second paper totally disappear'd."

In this experiment, the rays of light from the paper which has disappeared from view are received upon the punctum cæcum, at the point of entrance of the optic nerve. If the observer withdraw himself still farther, the second circle will reappear, as the rays are removed from the punctum cæcum. With the ophthalmoscope, the point of penetration of the optic nerve may be readily seen in the living eye. If the image of a flame be directed upon this point, the sensation of light is either not perceived or it is very faint and indefinite, and it is then probably due to diffusion to other portions of the retina.

The relative sensibility of different portions of the retina has been accurately measured by Volkmann and has been found to be in an inverse ratio equal to about the square of the distance from the axis of most perfect vision. This observer calculated the distance between the sensitive elements of the retina at which he supposed that two parallel lines would appear as one. In the axis of vision, the distance was 0·00029", and, at a deviation inward of 8°, it was 0·03186", a diminution of acuteness of more than a hundred times. The following table gives the results of these experiments:

Angle of deviation of the object seen, from the visual axis inward.	Calculated distance, for the retinal elements, of the parallel lines.
0°	0·00029″
1°	0·00055″
2°	0·00091″
3°	0·00141″
4°	0·00153″
5°	0·00180″
6°	0·00383″
7°	0·01527″
8°	0·03186″

This table illustrates, with great exactness, the gradual diminution in the acuteness of vision as the impressions are made farther and farther from the visual axis. The experiments were made upon the same principle as that of observations upon the tactile sensibility of different portions of the skin by testing the power of distinguishing the two points of the æsthesiometer.

The fact of the formation of images upon the retina, which are exact only at or immediately surrounding the fovea centralis, being settled, it remains to see how these images are rendered perfect, and to study the mechanism of refraction by the transparent media of the eye.

Mechanism of Refraction in the Eye.

A visible object sends rays from every point of its surface to the cornea. If the object be near, the rays from each and every point are divergent as they strike the eye. Rays from distant objects are practically parallel. It is evident that the refraction for diverging rays must be greater than for parallel rays, as a necessity of distinct vision; in other words, the eye must be accommodated for vision at different distances. Leaving, however, the mechanism of accommodation for future consideration, we shall endeavor to show how the rays of light as they penetrate the eye are refracted and brought to a focus at the retina.

The important agents in refraction in the eye are the surfaces of the cornea and the crystalline lens. Careful calculations have shown that the index of refraction of the aqueous humor is sensibly the same as that of the substance of the cornea, so that, practically, the refraction is the same as if the cornea and the aqueous humor were one and the same substance. The index of refraction of the vitreous humor is practically the same as that of the aqueous humor, both being about equal to the index of refraction of pure water. Refraction by the crystalline lens, however, is more complex in its mechanism; depending, first, upon the curvatures of its two surfaces, and, again, upon the differences in the consistence of different portions of its substance. In view of these facts, we may simplify the conditions of refraction in the eye by assuming the following arrangement:

The cornea presents a convex surface upon which the rays of light are received. At a certain distance behind its anterior border, is the crystalline, a double-convex lens, corrected, sufficiently for all practical purposes, both for spherical and chromatic aberration. This lens is practically suspended in a liquid with an index of refraction equal to that of pure water; as both the aqueous humor in front and the vitreous humor behind have the same refractive power. Behind the lens, in its axis and exactly in the plane upon which the rays of light are brought to a focus by the action of the cornea and the lens, is the fovea centralis, which is the centre of distinct vision. The anatomical elements of the fovea are capable of receiving visual impressions, which are conveyed to the brain by the optic nerves. All impressions made upon other portions of the retina are comparatively indistinct; and the point of entrance of the optic nerve is insensible to light. Inasmuch as the punctum cæcum is situated in either eye upon the nasal side of the retina, in normal vision, rays from the same object cannot fall upon both points at the same time. Thus, in binocular vision, the insensibility of the punctum cæcum does not interfere with sight; and the movements of the globe prevent any notable interference in vision, even with one eye. The sclerotic coat is for the protection of its contents and for the insertion of muscles. The iris has an action similar to that of the diaphragm in optical instruments. The suspensory ligament of the lens, the ciliary body, and the ciliary muscle, are for the fixation of the lens and its accommodation to distinct vision at different distances. The choroid is a dark membrane for the absorption of light, preventing confusion of vision from reflection within the eye.

Refraction by the cornea is effected simply by its external surface. The rays of light from a distant point are deviated by its convexity so that, if they were not again refracted by the crystalline lens, they would be brought to a focus at a point situated about $\frac{4}{10}$ of an inch behind the retina. Without the crystalline lens, therefore, distinct, unaided vision is generally impossible, although the sensation of light is appreciated. In cases of extraction of the lens for cataract, the crystalline is supplied by a convex lens placed before the eye.

The rays of light, refracted by the anterior surface of the cornea, are received upon the anterior surface of the crystalline lens, by which they are still farther refracted. Passing through the substance of the lens, they undergo certain modifications in refraction dependent upon the differences in the various strata of the lens. These modifications have not been accurately calculated; but it is sufficient to state that they contribute to the accuracy of the formation of the retinal image and to the production of an image practically free from chromatic dispersion. As the rays pass out of the crystalline lens, they are again refracted by its posterior curvature and are brought to a focus at the area of distinct vision.

The rays from all points of an object distinctly seen are brought to a focus, if the accommodation of the lens be correct, upon a restricted surface in the macula lutea; but the rays from different points cross each other before they reach the retina, and the image is consequently inverted. This is a fact capable of actual demonstration, as we have shown in treating of the formation of images in the eye.

Calculating the curvatures of the refracting surfaces in the eye and the indices of refraction of its transparent media, it has been pretty clearly shown, by mathematical formulæ, that the eye, viewed simply as an optical instrument, and not practically, as the organ of vision, presents a certain degree of spherical and chromatic aberration; but with these formulæ we have little to do in our purely physiological consideration of vision.

In most calculations of the size of images, the positions of conjugate foci, etc., in normal and abnormal eyes, a schematic eye reduced by Donders, after the example of Listing, is regarded as sufficiently exact for all practical purposes. This simple scheme represents the eye as reduced to a single refracting surface, the cornea, and a single liquid assumed to have an index of refraction equal to that of pure water. The distance between what are called the two nodal points and between the two principal points of the dioptric system of the eye is so small, amounting to hardly $\frac{1}{100}$ of an inch, that it can be neglected. In this simple eye, we assume a radius of curvature of the cornea of about $\frac{1}{5}$ of an inch, and have a single optical centre situated $\frac{1}{5}$ of an inch back of the cornea, the "principal point" being in the cornea, at the axis of vision. The posterior focal distance, that is, the focus, at the bottom of the eye, for rays that are parallel in the air, is about $\frac{4}{5}$ of an inch. The anterior focal distance, that is, for rays parallel in the vitreous humor, is about $\frac{3}{5}$ of an inch. The measurements in this simple schematic eye can be easily remembered and used in calculations.

Astigmatism.

We have already alluded to an important peculiarity in the optical apparatus; which is that the visual line does not coincide exactly with the axis of the eye. There is still another normal deviation from mathematical exactness in the refraction of rays by the cornea and the crystalline lens, which is of considerable importance. If we place before the eyes two threads crossing each other at right angles in the same plane, one of these threads being vertical, and the other, horizontal, when the optical apparatus is adjusted so that one line is seen with perfect distinctness, the other is not well defined. In other words, when we accommodate for the vertical thread, the horizontal is indistinct, and *vice versa*. If the horizontal line be seen distinctly, in order to see the vertical without modifying the accommodation, it must be removed to a greater distance. This depends chiefly upon a difference in the vertical and the horizontal curvatures of the cornea, so that the horizontal meridian has a focus slightly different from the focus of the vertical meridian. A condition opposite to that observed in the cornea usually exists in the crystalline lens; that is, the difference which exists between the curvatures of the lens in the vertical and the horizontal meridians is such that the deepest curvature in the lens is situated in the meridian of the shallowest curvature of the cornea. In this way, in normal eyes, the aberration of the lens has a tendency to correct the aberration in the cornea; but this correction is incomplete, and there still remains, in all degrees of tension of accommodation, a marked difference in the vision as regards vertical and horizontal lines.

The condition just described is known under the name of normal, regular astigmatism; but the aberration is not sufficiently great to interfere with distinct vision. The degree of regular astigmatism presents normal variations in different eyes. In some eyes there is no astigmatism; but this is rare. According to Donders, if the astigmatism amount to $\frac{1}{40}$ or more, it is to be considered abnormal; which simply means that, beyond this point, the aberration interferes with distinct vision.

From the mere definition of regular astigmatism, it is evident that this condition and the degree to which it exists may easily be determined by noting the differences in the foci for vertical and horizontal lines, and it may be exactly corrected by the application of cylindrical glasses of proper curvature. Indeed, the curvature of a cylindrical glass which will enable a person to distinguish vertical and horizontal lines with perfect distinctness at the same time is an exact indication of the degree of aberration. Regular astigmatism, such as we have described, may be so exaggerated as to interfere very seriously with vision, when it becomes abnormal. This kind of aberration, however, which is dependent upon an abnormal condition of the cornea, is remediable by the use of properly-adjusted cylindrical glasses.

Irregular astigmatism, excluding cases of pathological deformation, opaque spots, etc., in the cornea, depends upon irregularity in the different sectors of the crystalline lens. Instead of a simple and regular aberration, consisting in a difference between the depth of the vertical and the horizontal curvatures of the cornea and lens, we have irregular variations in the curvatures of different sectors of the lens. As a consequence of this, when the irregularities are very great, there is impairment of the sharpness of vision. The circles of diffusion, which are regular in normal vision, become irregularly radiated, and single points appear multiple, an irregularity described under the name of polyopia monocularis. Accurate observations have shown that this condition exists to a very moderate degree in normal eyes; but it is so slight as not to interfere with ordinary vision. In what is called normal, irregular astigmatism, the irregularity depends entirely upon the crystalline lens. If we place before the eye a card, with a very small opening, and move this before the lens, so that the pencil of light falls successively upon different sectors, it can be shown that the focal distance is different for different portions. The radiating lines of light observed in looking at remote luminous points, as the fixed stars, are produced by this irregularity in the curvatures of the different sectors of the lens.

While regular astigmatism, both normal and abnormal, may be perfectly corrected by placing cylindrical glasses before the eyes, it is impossible, in the great majority of cases, to construct glasses which will remedy the irregular form.

Movements of the Iris.

The movements of the iris are sufficiently simple, as well as the physiological conditions under which they take place; and it is only when we come to study the exact mechanism of the production of these movements through the nervous system, that the subject becomes complex, and, to a certain extent, obscure. As regards the movements themselves, the simple facts are as follows:

There are two physiological conditions under which the size of the pupil is modified: The first of these depends upon the amount of light to which the eye is exposed. When the quantity of light is small, the pupil is widely dilated, so as to admit as much as possible to the retina. When the eye is exposed to a bright light, the retina is protected by contraction of the iris. The muscular action by which the iris is contracted is characteristic of the smooth muscular fibres, as can be readily seen by exposing an eye, in which the pupil is dilated, to a bright light. Contraction does not take place instantly, but an appreciable interval elapses after the exposure, and a more or less gradual diminution in the size of the pupil is observed. This is seen both in solar and in artificial light. The second of these conditions depends, indirectly, upon the voluntary action of muscles. We have already seen, in connection with the physiology of the third pair of nerves, that the effort of converging the axes of the eyes by looking at a very near object contracts the pupils. We shall see, also, that the effort of accommodation of the eye for near objects produces the same effect, even when the eyes are not converged. This action will be fully considered under the head of accommodation.

One point relating to the anatomy of the iris is of great importance in connection with the physiology of its movements; and that is the question of the existence of dilator fibres. Upon this point there is some difference of opinion; but, as we stated in treating of the structure of the eye, the weight of anatomical authority is decidedly in favor of the existence of radiating fibres.

Direct Action of Light upon the Iris.—The variations in the size of the pupil under different physiological conditions are effected almost exclusively through the nervous system, either by reflex action from variations in the intensity of light, or by a direct influence, as in accommodation for distances; but it is nevertheless true that the muscular tissue of the iris will respond directly to the stimulus of light. Harless noted, in subjects dead of various diseases, from five to thirty hours after death, that the iris contracted under the stimulus of light; and he justly remarks that this is probably due to direct action upon its muscular tissue, and that it is not reflex, for the reason that the irritability of the nerves in warm-blooded animals disappears certainly in twenty hours after death. The experiments of Harless were made upon the two eyes, one being exposed to the light, while the other was closed. The contraction, however, took place very slowly, requiring an exposure of several hours. This mode of contraction is very different from the action of the iris during life, but it is precisely like the contraction observed after division of the motor oculi communis, which is slow and gradual and undoubtedly depends upon the direct action of light upon the muscular fibres.

Action of the Nervous System upon the Iris.—This subject, as far as it relates to the third pair, has been pretty fully considered in connection with the physiology of these nerves; and it is unnecessary to refer again in detail to the experiments which have already been cited. The reflex phenomena observed are sufficiently distinct. When light is admitted to the retina, the pupil contracts, and the same result follows mechanical irritation of the optic nerves. When the third pair of nerves has been divided, no such reflex phenomena are observed. It is well known, also, that division of the third nerves in the lower animals or their paralysis in the human subject produces permanent dilatation of the pupil, the iris responding, only in the slow and gradual manner already indicated, to the direct action of light.

Taking all the experimental facts into consideration, it is certain that the third nerve has an important influence upon the iris. Filaments from the ophthalmic ganglion animate the circular fibres, or sphincter, and these filaments derive their power from the third cranial nerve. If this nerve be divided, the iris becomes permanently dilated and is immovable, except that it responds very slowly to the direct action of light. The reflex action by which the pupil is contracted under the stimulus of light operates through the third nerve, and no such action can take place after this nerve has been divided. In view of these facts, there can be no doubt with regard to the nervous action upon the sphincter of the pupil, this muscle being animated exclusively by filaments from the motor oculi communis, coming through the ophthalmic ganglion.

We admit, with most modern anatomists, the existence of radiating muscular fibres in the iris, the action of which is antagonistic to the circular fibres, and which dilate the pupil. That these fibres are subjected to nervous influence is rendered certain by experiments upon the sympathetic system.

The effects of division of the sympathetic in the neck have been treated of fully in connection with the general functions of these nerves. It will be sufficient for our present purposes to state, in a general way, the influence of these nerves upon the movements of the iris. There can be no doubt that the action of the sympathetic upon the pupil is directly antagonistic to that of the third pair, the former presiding over the radiating, or dilating muscular fibres; and the only question to determine is the course taken by the sympathetic filaments to the iris. Experiments on the influence of the fifth pair upon the pupil have been somewhat contradictory in different animals. In rabbits, section of this nerve in the cranial cavity produces contraction of the pupil; but in dogs and cats the same operation produces dilatation. In the human subject, of course, it is impossible to determine this point by direct experiment; and the varying results obtained in observations upon different animals probably depend upon differences in the anatomical relations of the nerves. It is probable, however, that the filaments of the sympathetic which animate the dilator fibres join the fifth nerve near the ganglion of Gasser and from this nerve pass to the iris.

There seem to be two distinct nerve-centres corresponding to the two sets of nerves which regulate the movements of the iris. One of these centres presides over the reflex contractions of the iris, and the other is the centre of origin of the nervous influence through which the pupil is dilated.

The mechanism of reflex contraction of the iris under the stimulus of light is sufficiently simple. An impression is made upon the retina, which is conveyed by the optic nerves to the centre of vision, and, in obedience to this impression, the sphincter of the iris contracts. If the optic nerves be divided, so that the impression cannot be conveyed to the centre, or if we divide the third pair, through which the motor stimulus is conveyed to the muscular fibres, no movements of the iris can take place. The centres which preside over these reflex phenomena are situated in the tubercula quadrigemina. In the remarkable experiments of Flourens upon the encephalic centres, it was shown that the iris loses its mobility after destruction of the tubercula. This fact has been repeatedly confirmed by later experimenters. In birds, in which the decussation of the optic nerves is complete, this action is crossed, destruction of the tubercle upon one side producing immobility of the iris upon the opposite side; but in man, where the anatomical relations of the optic nerves upon the two sides are more complex, the crossed action is probably not so complete. In man, the axes of both eyes are habitually brought to bear upon objects, and it is well known that there is a physiological unity in the action of the two eyes in ordinary vision. We also observe that, when one eye only is exposed to light, the pupil becoming contracted under this stimulus, the pupil of the other eye also contracts. There is, indeed, a direct contraction and dilatation of the pupil of the eye which is exposed to the light, and an indirect, or "consensual" movement of the iris upon the opposite side. The consensual contraction occurs about $\frac{2}{5}$ of a second later than the direct action, and the consensual dilatation, about $\frac{1}{2}$ of a second later. (Donders.)

Budge and Waller have shown that the filaments of the sympathetic which produce dilatation of the pupil take their origin from the spinal cord. In the spinal cord, between the sixth cervical and the second thoracic nerves, is situated the inferior cilio-spinal centre. When the spinal cord is stimulated in this situation, both pupils become dilated. If the cord be divided longitudinally and the two halves be separated from each other by a glass plate, stimulation of the right half produces dilatation of the right pupil, and *vice versa.* This does not occur when the sympathetic in the neck has been divided. In addition to the inferior cilio-spinal centre, there is a superior centre, which is in communication with the superior cervical ganglion and is situated near the sublingual nerve. The influence of this centre over the pupil cannot be demonstrated by direct stimulation, because it is too near the origin of the fifth, irritation of which has an influence over the iris; but it is shown by division of its filaments of communication with the iris.

Section and galvanization of the different nerves which regulate the movements of the iris have a certain influence upon its vascularity; and, indeed, it has been thought that contraction is in a measure due to congestion of its vessels, and dilatation, to an opposite condition. This view is adopted by some of those who deny the existence of the radiating muscular fibres of the iris. Assuming that the size of the pupil is, to a certain extent, affected by the condition of the vessels, it is evident that the more extensive movements of the iris are due mainly to muscular action. It has been also shown that the changes in the iris produced by injection of its vessels are not to be compared in their extent with its physiological movements. The changes in vascularity produced by dividing or galvanizing the sympathetic do not differ from the phenomena noted in experiments upon other portions of the sympathetic system.

Accommodation of the Eye to Vision at Different Distances.

The mechanism by which the eye is adjusted for distinct vision at different distances is one of the most interesting and important points connected with the physiology of the sight. At the present day, this point may be regarded as definitely settled, particularly since the variations in the thickness and the curvatures of the crystalline lens have been so accurately measured by Helmholtz. We shall have little to say with regard to the various theories of accommodation advanced by the older physiologists, except to indicate, in a very general way, the most plausible views that have been adopted from time to time by physiological writers. In the first place, we shall note certain physical laws and their application to the eye, which show the necessity for accommodation.

Supposing the eye to be adapted to vision at an infinite distance, in which the rays from an object, as they strike the cornea, are practically parallel, it is evident that the foci of the rays, as they form a distinct image upon the retina, are all situated at the proper plane. Under these conditions, in a perfectly normal eye, the image, appreciated by the individual or seen by means of the ophthalmoscope, is perfectly clear and distinct. If the foci be situated in front of the retina, the rays, instead of coming to a focus upon a point in the retina, will cross, and, from their diffusion or dispersion, will produce indistinct vision. Under these circumstances, a distinct point is not perceived, but every point in the image is surrounded by an indistinct circle. These are called "circles of diffusion." If, now, the eye, adjusted for vision at an infinite distance, be brought to bear upon a near object, the rays from which are divergent as they strike the cornea, the image will be no longer distinct, but will be obscured by circles of diffusion. It is the adjustment by which these circles of diffusion are removed that constitutes accommodation. This fact has been demonstrated by Helmholtz by means of the ophthalmoscope. "If the eye be adjusted to the observation of an object placed at a certain distance, it is found that the image of a flame, placed at the same distance, is produced with perfect distinctness upon the retina, and, at the same time, upon the illuminated plane of the image, the vessels and the other anatomical details of the retina are seen with equal distinctness. But, when the flame is brought considerably nearer, its image becomes confused, while the details of the structure of the retina remain perfectly distinct."

It is evident that there is a certain condition of the eyes adapted to vision at an infinite distance, and that, for the distinct perception of near objects, the transparent media must be so altered in their arrangement or in the curvatures of their surfaces, that the refraction will be greater; for, without this, the rays would be brought to a focus beyond the retina.

The changes in the eye by which accommodation is effected are now known to consist mainly in an increased convexity of the lens for near objects; and the only points in dispute are a few unimportant details in the mechanism of this action. The simple facts to be borne in mind in studying this question are the following:

When the eye is accommodated to vision at an infinite distance, the parts are passive.

In the adjustment of the eye for near objects, the convexities of the lens are increased by muscular action.

In accommodation for near objects, the pupil is contracted; but this action is merely accessory and is not essential.

The ordinary range of accommodation varies between a distance of about five inches and infinity.

Changes in the Crystalline Lens in Accommodation.—It is important to determine first the extent and nature of the changes of the lens in accommodation; and, by the ingenious experiments of the German physiologists, particularly those of Helmholtz, these changes have been accurately measured in the living subject. As the general result of these measurements, it was ascertained that the lens becomes increased in thickness in accommodation for near objects, chiefly by an increase in its anterior curvature, by which this surface of the lens is made to project toward the cornea. As the iris is in contact with the anterior surface of the lens, this membrane is made to project in the act of accommodation. The posterior curvature of the lens is also increased, but this is slight as compared with the increase of the curvature of its anterior surface. The distance between the posterior surface of the lens and the cornea is not sensibly altered. It is unnecessary to describe minutely the methods employed in making these calculations, and it is sufficient for our purposes to state that it is done by accurately measuring the comparative size of images formed by reflection from the anterior surface of the lens. The results obtained by Helmholtz in observations upon three different persons are as follows:

Persons examined.	Radius of curvature of the anterior surface of the lens.		Displacement of the pupil in accommodation for near objects.
	Distant vision.	Near vision.	
O. H.	0·4641 of an inch.	0·3354 of an inch.	0·0140 of an inch.
B. P.	0·3432 "	0·2701 "	0·0172 "
J. H.	0·4056 "		

The mechanism of the changes in the thickness and in the curvatures of the lens in accommodation can only be understood by keeping clearly in mind the physical properties of the lens itself and its anatomical relations. *In situ*, in what has been called the indolent state of the eye, the lens is adjusted to vision at an infinite distance and is flattened by the tension of its suspensory ligament. After death, indeed, it is is easy to produce changes in its form by applying traction to the zone of Zinn. If we remember, now, the exact relations of the suspensory ligament, the ciliary muscle, and the lens, and keep in mind the tension within the globe, it is evident that, when the ciliary muscle is in repose, the capsule will compress the lens, increasing its diameter and diminishing its convexity. It is in this condition that the eye is adapted to vision at an infinite distance. It is evident, also, that very slight changes in the convexity of the lens will be sufficient for the range of accommodation required. If we fix with the eye any near object we are conscious of an effort, and the prolonged vision of near objects produces a sense of fatigue. This may be illustrated by the very familiar experiment of looking at a distant object through a gauze. When the object is seen distinctly, the gauze is scarcely perceived; but by an effort we can bring the eye to see the meshes of the gauze distinctly, when the impression of the distant object is either lost or becomes very indistinct.

Our knowledge of the action of the ciliary muscle is only to be arrived at theoretically and by studying the effects produced upon the lens. This muscle, it will be remembered, arises from the circular line of junction of the cornea and sclerotic, which is undoubtedly its fixed point, passes backward, and is lost in the tissue of the choroid, extending as far back as the anterior border of the retina. Most of the fibres pass directly backward, but some become circular or spiral. When this muscle contracts, the choroid is drawn forward, with, probably, a slightly spiral motion of the lens, the contents of the globe situated posterior to the lens are compressed, and the suspensory ligament is relaxed. The lens itself, the compressing and flattening action of the suspensory ligament being diminished, becomes thicker and more convex, by virtue of its own elasticity, in the same way that it becomes thicker after death when the tension of the ligament is artificially diminished.

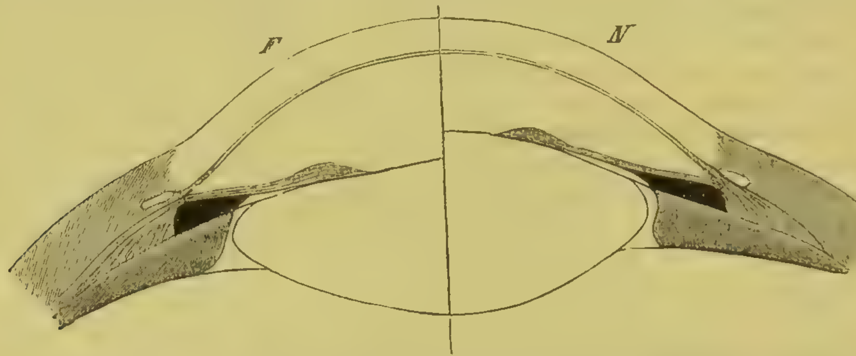


FIG. 253.—*Section of the lens, etc., showing the mechanism of accommodation.* (Fick.)
The left side of the figure (*F*) shows the lens adapted to vision at infinite distances; the right side of the figure (*N*) shows the lens adapted to the vision of near objects, the ciliary muscle being contracted and the suspensory ligament of the lens consequently relaxed.

This is, in brief, the mechanism of accommodation. Near objects are seen distinctly by a voluntary contraction of the ciliary muscle, the action of which is adapted to the requirements of vision with exquisite nicety. In early life, the lens is soft and elastic, and the accommodating power is at its maximum; but in old age the lens becomes flattened, harder, and less elastic, and the power of accommodation is necessarily diminished.

Changes in the Iris in Accommodation.—The size of the pupil is sensibly diminished in accommodation of the eye for near objects. Although the movements of the iris are directly associated with the muscular effort by which the form of the lens is modified, the contraction of the pupil is not one of the essential conditions of accommodation. Helmholtz cites a case in which the iris was completely paralyzed, the power of accommodation remaining perfect; and he mentions another case, reported by Von Graefe, in which accommodation was not disturbed after loss of the entire iris.

We have already noted the fact that the pupil contracts when the eyes are made to converge by the action of the muscles animated by the third pair of nerves; and it is evident that convergence of the eyes always occurs in looking at very near objects. It becomes a question, then, whether the contraction of the pupil in accommodation for near objects be associated with the action of the third nerves, or with filaments from the ophthalmic ganglion, which supplies the nervous influence to the ciliary muscle. This seems to have been definitively settled by Donders, who demonstrated two important points: First, that increased convergence of the visual lines without change of accommodation makes the pupil contract, as is easily proven by simple experiments with prismatic glasses. Second, that when accommodation is effected without converging the visual axes, "each stronger tension is combined with contraction of the pupil."

The action of the iris, as is evident from the facts just stated, is to a certain extent under the control of the will; but it cannot be disassociated, first, from the voluntary action of the muscles which converge the visual axes, and second, from the action of the ciliary muscle. Donders states that, by alternating the accommodation for a remote and a near object, he could voluntarily contract and dilate the pupil more than thirty times in the minute. Brown-Séquard, in discussing the voluntary movements of the iris, mentions a case in which "the pupil could be contracted or dilated without changing the position of the eye or making an effort of adaptation for a long or a short distance." As a farther evidence of the connection of accommodation with muscular action, cases are cited in works on ophthalmology, in which there is paralysis of the ciliary muscle as well as cases in which the act of accommodation is painful.

An interesting phenomenon connected with accommodation is observed in looking at a near object through a very small orifice, like a pinhole. The shortest distance at which we can see a small object distinctly is about five inches; but, if we look at the same object through a pinhole in a card, it can be seen distinctly at the distance of about one inch, and it then appears considerably magnified. In this experiment, the card serves as a diaphragm with a very small opening, so that the centre of the lens only is used; and the apparent increase in the size of the object is probably due to the fact that its distance from the eye is many times less than the distance at which distinct vision is possible under ordinary conditions. It is well known that myopic persons, by being able to bring the eye nearer to objects than is possible in ordinary vision, can see minute details with extraordinary distinctness.

Erect Impressions produced by Images inverted upon the Retina.

If we have become thoroughly acquainted with the mechanism of the formation of images upon the retina and the physiological action of the different parts of the optical apparatus, it will be sufficient to note the action of both eyes, as contrasted with the action of one, in normal vision, without discussing fully the multitude of curious observations made with the stereoscope; and we can readily comprehend the action of muscles by which the axis of vision is directed toward different objects, without entering into a discussion of abstruse mathematical calculations with regard to the exact centre of rotation, the law of torsions, and other points connected with physiological optics. These are questions, however, of great interest to ophthalmologists and are fully discussed in elaborate special treatises.

We shall allude briefly, in this connection, to a question which has long engaged the attention of physiologists, and one which, we cannot but think, has been made the subject of much unprofitable speculation. It is a matter of positive demonstration that the images of objects seen are inverted as they appear upon the retina. Why is it, however, that objects are appreciated as erect, when their images are thus inverted? With a knowledge of the fact that the appreciation of impressions made upon the nerves of special sense is capable of education and is corrected by experience, it seems hardly necessary to enter into an elaborate discussion of this point. We appreciate with accuracy the density of objects, the direction of sounds, differences in musical tones, the taste of sapid substances, odors, etc., as the result, to a great degree, of education. In the same way, probably, we acquire the power of noting the position of objects in vision; but even this supposition is not necessary to explain the phenomenon of direct vision by means of inverted images. The following paragraph, quoted from Giraud-Teulon, is a simple expression of facts and shows the absurdity of the elaborate theoretical explanations made by many of the earlier writers:

"If the objects seen mark their image upon the retina, each one in a proper secondary axis; if, on the other hand, the retina appreciates these, *independently of ourselves*, in these same secondary axes, which all cross at the same point, it is evident that an exact or *erect* sensation, as well as the object which produces it, should necessarily correspond to an inverted or reversed image. But it is neither habit, education, nor information derived from the sense of touch, that enables us, as it is said, to see objects *erect* by means of *reversed images*. The retina sees or localizes objects where they are; that is what we call 'erect.' If the picture be reversed, it is a mere matter of geometry."

In discussing the same question, Helmholtz says that "our natural consciousness is completely ignorant even of the existence of the retina and of the formation of images: how should it know any thing of the position of images formed upon it?"

Binocular Vision.

We have thus far considered the mechanism of the eye and its action as an optical instrument, in simple, or monocular vision. It is evident, however, that we habitually use both eyes, and that their axes are practically parallel in looking at distant objects and are converged when objects are approached to the nearest point at which we have distinct vision. In fact, an image is formed simultaneously upon the retina of each eye, but it is nevertheless appreciated as a unit. If the axis of one eye be slightly deviated by pressure upon the globe, so that the images are not formed upon corresponding points upon the retina of each eye, our vision is more or less indistinct and is double. In strabismus, when this condition is recent, temporary, or periodical, as in recent cases of paralysis of the external rectus muscle, when both eyes are normal, there is double vision. When the strabismus is permanent and has existed for a long time, double vision may not be observed, unless the subject direct the attention strongly to this point. As it is usual, in such cases, for one eye to be much superior to the other in acuteness of vision, an object is fixed with the better eye, and its image is formed upon the fovea. The image formed upon the retina of the other eye is indistinct, and in many instances it is habitually disregarded; so that, practically, the subject uses but one eye, and presents the errors of appreciation which attend monocular vision, such as a want of accurate estimation of the solidity and distance of objects. It is stated as the rule that, when strabismus of long standing is remedied, as far as the axes of the eyes are concerned, by an operation, binocular vision is not restored; but the experiments necessary to the accurate determination of this point are exceedingly delicate and must be made with great care. This is explained upon the supposition that the functional power of the retina of the affected eye has been gradually and irrecoverably lost from disuse. In normal binocular vision, the images are formed upon the fovea centralis of each eye; that is, upon corresponding points, which are, for each eye, the centres of distinct vision.

It is hardly necessary to speculate with regard to the reason why two images, one upon each retina, convey the impression of a single object. We appreciate a sound with both ears; the impression of a single object is received by the sensory nerves of two or more fingers; the olfactory nerves upon the two sides are simultaneously concerned in olfaction; and, in the same way, when we look at a single object with both eyes, the brain appreciates a single image. We shall see, however, that the concurrence of both eyes is necessary to the exact appreciation of distance and form; and, when the two images are formed upon corresponding points, the brain receives a correct impression of a single object. When our vision is perfectly normal, the sensation of the situation of any single object is referred to one and the same point; and we cannot receive the impression of a double image unless the conditions of vision be abnormal.

Corresponding Points.—While it requires no argument, after the statements we have just made, to show that an image must be formed upon the fovea of each eye in order to produce the effect of a single object, it becomes important to ascertain how far it is necessary that the correspondence of points be carried out in the retina. This leads to considerations of very great interest and importance. It is almost certain that, for absolutely perfect, single vision with the two eyes, the impressions must be made upon exactly corresponding points, even to the ultimate sensitive elements of the retina. We may suppose, indeed, that each rod and each cone of one eye has its corresponding rod and cone in the other, situated at exactly the same distance in corresponding directions from the visual axis. When the two images of an object are formed upon these corresponding points, they appear as one; but, when the images do not correspond, the impression is as though the images were formed upon different points in one retina, and, of necessity, they appear double.

The effect of a slight deviation from the corresponding points may be illustrated by the following experiment: We fix a small object, like a lead-pencil, held at a distance of a few inches, with the eyes, and see it distinctly as a single object; we hold in the same line, a few inches farther removed, another small object; when the first is seen distinctly, the second appears double; we fix the second with the eyes, and the first appears double. It is evident here, that, when the axes of the eyes bear upon one of these objects, the images of the other must be formed at a certain distance from the corresponding retinal points.

The Horopter.—The above-mentioned experiment enables us to understand the situation of the horopter. If we fix both eyes upon any object directly in front and keep them in this position, a similar object moved to one side or the other, within a certain area, may be seen without any change in the direction of the axis of vision; but the distance from the eye at which we have single vision of this second object is fixed, and, at any other distance, the object appears double. The explanation of this is, that, at a certain distance from the eye, the images are formed upon corresponding points in the retina; but, at a shorter or longer distance, this cannot occur. This illustrates the fact that there are corresponding points throughout the sensitive layer of the retina, as well as in the fovea centralis. By these experiments, the following facts have been ascertained: With both eyes fixed upon an object, another object moved to one side or the other can be distinctly seen only when it is carried in a certain curved line. On either side of this line, the object appears double. This line, or area, for the line may have any direction, is called the horopter. It was supposed at one time to be a regular curve, a portion of a circle drawn through the fixed point and the points of intersection of the rays of light in each eye. Although it has been ascertained that the line varies somewhat from a regular curve, and also varies in different meridians, this is due to differences in refraction, etc., and the principle is not altered.

It is undoubtedly true that education and habit have a great deal to do with the correction of visual impressions and the just appreciation of the size, form, and distance of objects. If we may credit the account of the remarkable case of Caspar Hauser, who is said to have been kept in total darkness and seclusion, from the age of five months until he was nearly seventeen years old, the appreciation of size, form, and distance is acquired by correcting and supplementing the sense of sight by experience, even in binocular vision. This boy at first had no idea of the form of objects, or of distance, until he had learned by touch, by walking, etc., that certain objects were round, others square, and had actually traversed the distance from one object to another. At first, all objects appeared to be, as it were, painted upon a screen. Such points as these it would be impossible for us to accurately observe in infants; but we have all seen young children grasp at remote objects, apparently under the impression that they were within reach. It must be admitted, however, that the case of Casper Hauser is rather indefinite; but it is certain that, even in the adult, education and habit enable us to greatly improve the faculty of estimating distances.

The important questions for us now to determine relate to the differences between monocular and binocular vision in the adult. We may see an object distinctly with one eye; but are we able, from an image made upon one retina, to appreciate all its dimensions and its exact locality?

Accurate observations bearing upon this question leave no doubt of the fact that monocular vision is incomplete and inaccurate, and that it is only when two images are formed, one upon each retina, that vision is perfect. We cannot better illustrate the truth of this proposition and the exact condition of our positive knowledge upon this important point, than by quoting in full the facts and arguments advanced by Giraud-Teulon:

"Monocular vision only indicates to us immediately *visual direction*, and not precise locality. At whatever distance a luminous point may be situated in the line of direction, it forms its image upon the same point in the retina.

"In the physiological action of a single eye, in order to arrive at an idea of the distance of a point in a definite direction, we have only the following elements:

"1. The consciousness of an effort of accommodation.

"2. Our own movement in its relations to the point observed.

"3. Facts brought to bear from recollection, education, our acquired knowledge with regard to the form and size of objects: in a word, experience.

"4. The geometric perspective of form and position.

"5. Aërial perspective.

"All these are elements wanting in precision and leaving the problem without a decisive solution.

"And, indeed:

"We place before one of our eyes, the other being closed, the excavated mould of a medallion: we do not hesitate, after a few seconds, to mistake it for the relief of the medallion. This illusion ceases at the instant that both eyes are opened.

"Or again:

"A miniature, a photograph, a picture, produces for a single eye a perfect illusion; but, if both eyes be open, the picture becomes flat, the prominences and the depressions are effaced.

"We may repeat the following experiment described by Malebranche: 'Suspend by a thread a ring, the opening of which is not directed toward us; step back two or three paces; take in the hand a stick curved at the end; then, closing one eye with the hand, endeavor to insert the curved end of the stick within the ring, and we shall be surprised at being unable to do in a hundred trials what we should believe to be very easy. If, indeed, we abandon the stick and endeavor to pass one of the fingers through the ring, we shall experience a certain amount of difficulty, although it is very near. This difficulty ceases at the instant that both eyes are opened.'

"As regards precision, exactitude of information concerning the relative distance of objects, that is to say, the idea of the *third dimension* or of *depth*, there is then a notable difference between binocular vision and that which is obtained by means of one eye alone."

It is evident that an accurate idea of the distance of near objects cannot be obtained except by the use of both eyes, and this fact will explain, in part, the errors of monocular vision, when we look with one eye upon objects in relief; for, under these conditions, we cannot determine with accuracy whether the points in relief be nearer or farther from the eye than the plane surface. This will not fully explain, however, the idea of solidity of objects which we obtain by the use of both eyes; for the estimation of distance is obtained by bringing the axes of both eyes to bear upon a single object, be it near or remote. The fact is, as was distinctly stated by Galen, in the second century that, when we look at any solid object not so far removed as to render the visual axes, practically parallel, we see with the right eye a portion of the surface which is not seen with the left eye, and *vice versa*. The two impressions, therefore, are not identical for each retina; the image upon the left retina including a portion of the left side of the object not seen by the right eye, the right image in the same way including a portion of the right surface not seen by the left eye. These slightly dissimilar impressions are fused, as it were, produce the impression of a single image, when vision is perfectly normal, and this gives the idea of relief or solidity, enabling us to appreciate exactly the form of objects, when they are not too remote.

The fact just stated is of course a mathematical necessity in binocular vision for near objects; but the actual demonstration of the fusion of two dissimilar images and the consequent formation of a single image giving the impression of solidity was made by the invention of the stereoscope, by Wheatstone. The principle of this instrument is very simple. Two pictures are made, representing a solid object, one viewed slightly from the right side, and the other, slightly from the left, so as to imitate the differences in the images formed upon the two retinæ. These pictures are so placed in a box that the image of one is formed upon the right retina, and the other, upon the left. When these conditions are accurately fulfilled, we see but a single image, and this conveys to the mind the perfect illusion of a solid object. Experiments with the stereoscope are so familiar that they need hardly be dwelt upon. With most persons, an apparatus is necessary to shut off disturbing visual impressions; but some individuals are able to fuse two images in this way, placed in proper position, without the aid of an instrument, by a simple effort of the will.

The invention of the stereoscope has led to many curious and interesting experiments, especially since the art of photography has enabled us to produce pictures in any position with absolute accuracy; but a simple statement of the principle upon which the instrument is constructed illustrates the mechanism of binocular vision in the appreciation of the form of objects. Experience, the aid of the sense of touch, etc., enable persons with but one eye to get a notion of form, but the impressions are never entirely accurate in this regard, although, from habit, this defect occasions little or no inconvenience. A striking illustration of these points is afforded by the binocular microscope, which, especially with low magnifying powers, produces a startling impression of relief.

As we have just remarked, the stereoscope affords a satisfactory explanation of the mechanism of the eye in the appreciation of the form of objects; but, notwithstanding this, a theory has been proposed, and is adopted by some writers, that we obtain an idea of form by rapidly and insensibly directing the eyes successively toward different points on the surface of objects. It is difficult to understand how the eye can make these rapid movements, but the question is definitively settled by a very simple fact demonstrated by Dove, Helmholtz, and others. In an article on visual perception, by Helmholtz, it is stated that stereoscopic effect is recognized when two pictures are seen illuminated by an electric spark, the duration of which does not amount to the four-thousandth part of a second, so short, indeed, that a falling body appears absolutely motionless. Under these conditions, displacement of the line of vision would seem to be impossible.

We shall conclude our discussion of binocular vision and the stereoscope with a brief account of some experiments upon the binocular fusion of colors, which are very curious, although they have no very important bearing upon the physiology of the eye in ordinary vision. Though an opposite opinion is held by some experimenters, Helmholtz, with many others, states that, when one color is seen with one eye and another color with the other eye, in the stereoscope, the impression is not of a single color resulting from the combination of the two. It is true that there is an imperfect mingling of the two colors, but this is very different from the resulting color produced by the actual fusion of the two. There is, in other words, a sort of confusion of colors, without the complete combination with which we are familiar in ordinary experiments. One additional point of interest, however, is that the binocular fusion of two pictures, unequally illuminated or of different colors, produces a single image of a peculiar lustre, even when both surfaces are dull. This may be very strikingly shown by making a stereoscopic combination of images of crystals, one with black lines on a white ground, and the other with white lines on a black ground. The resulting image has then the appearance of dark, brilliant crystals, like graphite.

Duration of Luminous Impressions.

The time necessary for vision is exceedingly short; so short, indeed, that it almost passes our powers of comprehension. Taking advantage of the very delicate methods of chronometric observations now employed by physicists, it has been shown by Prof. Rood, of New York, that the letters on a printed page are distinctly seen when illuminated by an electric spark, the duration of which was measured and found to be not more than forty billionths of a second. Inasmuch as the waves of light strike the eye at the rate of over five hundred millions of millions in a second, it is evident that, even in the period indicated by Prof. Rood, an immense number of waves have time to impinge upon the retina.

We have long been familiar with the fact that an impression made upon the retina endures for a length of time that can readily be measured, and that its duration bears a certain degree of relation to the intensity of the luminous excitation. If, after looking fixedly at a very bright object, we suddenly produce complete obscurity, the object is more or less distinctly seen after the rays have ceased to pass to the eye, and the image fades away gradually. When we produce a rapid succession of images, they may be, as it were, fused into one, as the spokes of a rapidly-revolving wheel are indistinct and produce a single impression. This is due to the persistence of the successive retinal impressions; for, if a revolving wheel, or even a falling body, be illuminated for the brief duration of an electric spark, it appears absolutely stationary, as the period of time necessary for perfectly distinct vision and the duration of the illumination are so short, that there is no time for any appreciable movement of the object. The familiar experiments made with revolving disks strikingly illustrate these points. In a disk marked with alternate radiating lines of black and white, the rays become entirely indistinguishable during rapid revolution, and the disk appears of a uniform color, such as would be produced by a combination of the black and white. Very beautiful effects of artificial combination of colors may be produced in this way, the resultant color appearing precisely as if the individual colors had been ground together. It is also interesting, in this connection, to note that the duration of retinal impressions varies considerably for the different colors. According to Emsmann, the duration for yellow is 0·25 of a second; for white, 0·25 of a second; for red, 0·22 of a second; and for blue, 0·21 of a second.

It is unnecessary to describe farther in detail the well-known phenomena which illustrate the point under consideration. The circle of light produced by rapidly revolving a burning coal, the track of a meteor, and other illustrations, are sufficiently familiar, as well as many scientific toys producing optical illusions of various kinds.

Irradiation.—It has been observed that luminous impressions are not always confined to the elements of the retina directly involved, but are sometimes propagated to those immediately adjacent. This gives to objects a certain degree of amplification, which is generally in proportion to their brightness. An illustration of this is afforded by the simple experiment of looking at two circles, one black on a white ground, and the other white on a black ground. Although the actual dimensions of the two circles are identical, the irradiation of rays from the white circle makes this appear the larger. In a circle with one half black and the other white, the white portion will appear larger, for the same reason. This deception increases sensibly when we look steadily at the object. These phenomena are due to what has been called by physiologists irradiation; and their explanation is very simple. It is probable that luminous impressions are never confined absolutely to those parts of the retina upon which the rays of light directly impinge, but that the sensitive elements immediately contiguous are always more or less involved. In looking at powerfully-illuminated objects, the irradiation is considerable, as compared with objects which send fewer luminous rays to the eye.

In experiments analogous to those just described, made with strongly colored objects, it has been observed that the border of irradiation takes a color complementary to that of the object itself. This is particularly well marked when the objects are steadily looked at for some time. Illustrations of this point also are very simple. If we looked fixedly at a red spot or figure on a white ground, we soon see surrounding the red object a faint areola of a pale green; or, if the image be yellow, the areola will appear pale blue. These appearances have been called accidental areolæ.

Movements of the Eyeball.

The eyeball nearly fills the cavity of the orbit, resting, by its posterior portion, upon a bed of adipose tissue, which is never absent, even in extreme emaciation. Outside of the sclerotic, is a fibrous membrane, the tunica vaginalis oculi, or capsule of Tenon, which is useful in maintaining the equilibrium of the globe. This fibrous membrane surrounds the posterior two-thirds of the globe and is loosely attached to the sclerotic. It is perforated by the optic nerve posteriorly, and by the tendons of the recti and oblique muscles of the eyeball in front, being reflected over these muscles. It is also continuous with the palpebral ligaments and is attached by two tendinous bands to the border of the orbit at the internal and the external angles of the lids.

The muscles which move the globe are six in number for each eye. These are, the external and internal recti, the superior and inferior recti, and the two oblique muscles. The four recti muscles and the superior oblique arise posteriorly from the apex of the orbit. The recti pass directly forward by the sides of the globe and are inserted by short, tendinous bands into the sclerotic, at a distance of from one-fourth to one-third of an inch from the margin of the cornea. The superior oblique, or trochlearis muscle passes along the upper and inner wall of the orbit to a point near the inner angle. It here presents a rounded tendon, which passes through a ring, or pulley of fibro-cartilage; and it is from this point that its action is exerted upon the globe. From the pulley, or trochlea, the tendon becomes flattened, passes outward and backward beneath the superior rectus, and is inserted into the sclerotic, about midway between the superior and the external rectus and just behind the equator of the globe. The inferior oblique muscle arises just within the anterior margin of the orbit, near the inner angle of the eye, and passes around the anterior portion of the globe, beneath the inferior rectus and between the external rectus and the eyeball, taking a direction outward and slightly backward. Its tendon is inserted into the sclerotic, a little below the insertion of the superior oblique. The general arrangement of these muscles is shown in Fig. 254.

The various movements of the eyeball are easily understood by a study of the associated movements of the muscles just enumerated, at least, as far as is necessary to the comprehension of the mechanism by which the eyes are directed toward any particular object. We have already seen that the centre of exact vision is in the fovea; and it is evident that, in order to see any object distinctly, it is necessary to bring it within the axes of vision of both eyes. As the globe is so balanced in the orbit as to be capable of rotation, within certain limits, in every direction, we have only to note the exact mode of action of each of the muscles, in order to comprehend how the different movements are accomplished; and it is sufficient for our purposes to admit that, approximatively, there is a common axis of rotation for each pair of muscles.

Under ordinary conditions, in the human subject, the action of the six ocular muscles is confined to the movements of rotation and torsion of the globe. It is said that, in the human subject, there is no such thing as protrusion of the eye from general relaxation of these muscles, and that it is impossible, by a combined action of the four recti muscles to retract the globe in the orbit; but those who have operated upon the eyes assert positively that this statement is erroneous, and that the globe is almost always suddenly and powerfully drawn within the orbit when a painful impression is made upon the cornea. This is stated as a matter of common observation by ophthalmic surgeons.

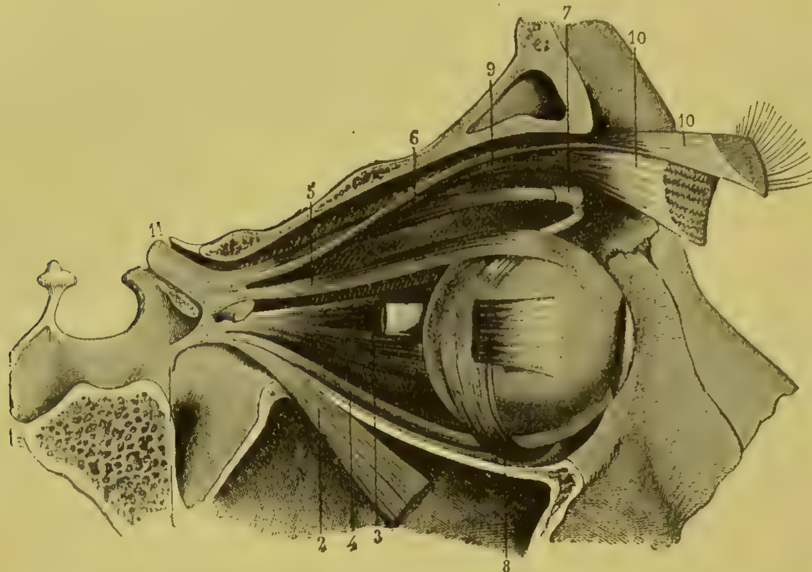


FIG. 254.—*Muscles of the eyeball.* (Sappey.)

1, attachment of the tendon connected with the inferior rectus, internal rectus, and external rectus; 2, external rectus divided and turned downward to expose the inferior rectus; 3, internal rectus; 4, inferior rectus; 5, superior rectus; 6, superior oblique; 7, pulley and reflected portion of the superior oblique; 8, inferior oblique; 9, levator palpebri superioris; 10, 10, middle portion of the levator palpebri superioris; 11, optic nerve.

The extent to which the line of vision may be turned by a voluntary effort varies in different individuals, even when the eyes are perfectly normal. In myopic eyes, the centre of rotation is deeper in the orbit than normal, and the extent of the possible deviation of the visual line is correspondingly diminished. Helmholtz states that, in his own person, with the greatest effort that he is capable of making, he can move the line of vision in the horizontal plane to the extent of about fifty degrees, and, in the vertical plane, about forty-five degrees; but he adds that these extreme rotations are very forced, and that they cannot be sustained for any length of time. It is probable that we seldom move the eyeball in any direction to an angle of forty-five degrees, the direction of the visual line being more easily accomplished by movements of the head.

Action of the Recti Muscles.—The action of the recti, particularly of the internal and external, is quite simple.

The internal and the external recti rotate the globe upon a vertical axis, which is perpendicular to the axis of the eye. The isolated action of these muscles, particularly of the external rectus, is often illustrated in certain forms of paralysis, which have been alluded to in connection with the history of the cranial nerves.

The superior and the inferior recti rotate the globe upon a horizontal axis, which is not at right angles with the axis of the eye, but is inclined from the nasal side slightly backward. The line which serves as the axis of rotation for these muscles forms an angle of about seventy degrees with the axis of the globe; and, as a consequence of this arrangement, their action is not so simple as that of the internal and external recti. The insertion of the superior rectus is such, that, when it contracts, the pupil is directed upward and inward, the inferior rectus directing the pupil downward and inward.

The above represents the simple, isolated action of each pair of recti muscles; but it is easy to see how, without necessarily involving the action of the oblique muscles, the globe may be made to perform an immense variety of rotations, and the line of vision may be turned in nearly every direction, by the action of the recti muscles alone.

Action of the Oblique Muscles.—Although there has been considerable discussion concerning the exact mode of action of the oblique muscles, their mechanism may now be regarded as pretty well settled, at least as regards the human subject. In the first place, it is sufficient for all practical purposes, to assume that the superior and the inferior oblique muscles act as direct antagonists to each other. The next point to determine is the direction of the axis of rotation of the globe with reference to the action of these muscles. The most exact, recent measurements show that this axis is horizontal and that it has an oblique direction from before backward and from without inward. The angle formed by the axis of rotation of the oblique muscles with the axis of the globe is thirty-five degrees; and the angle between the axis of the oblique muscles and the axis of the superior and inferior recti muscles is seventy-five degrees.

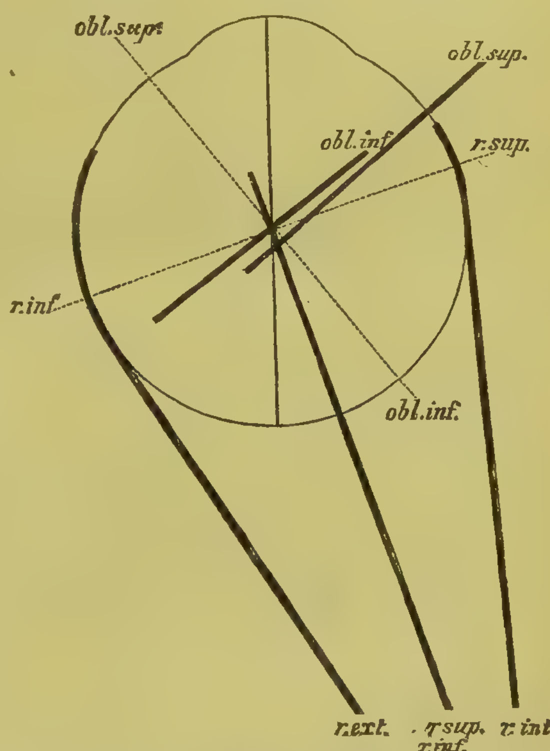


Fig. 255.—*Diagram illustrating the action of the muscles of the eyeball.* (Fick.)

The dark lines represent the muscles of the eyeball, and the dotted lines, the axis of the superior and the inferior rectus and the axis of the oblique muscles.

Given the direction of the axis of rotation and the direction of the superior oblique muscle, it is easy to understand the effects of its contraction. As this muscle, passing obliquely backward and forward over the globe, acts from the pulley near the inner angle of the eye to its insertion just behind the anterior half of the globe on its external and superior surface (7, Fig. 254), it must rotate the globe so as to direct the pupil downward and outward.

The inferior oblique, passing outward and slightly backward under the globe, acts from its origin at the margin of the orbit near the inner angle of the eye to its insertion, which is just below the insertion of the superior oblique. This muscle rotates the globe so as to direct the pupil upward and outward.

The action of the oblique muscles seems to be specially connected with the movements of torsion of the globe. It is necessary to distinct, single vision with both eyes, that the images should be formed upon exactly corresponding points on the retina, and that they should bear, for the two eyes, corresponding relations to the perpendicular. Thus it is that, when the head is inclined to one side, the eyes are twisted upon an oblique, antero-posterior axis; as can be readily observed if we watch little spots upon the iris during these movements.

The superior oblique muscle is supplied by a single nerve, the patheticus. When this muscle is paralyzed, the inferior oblique acts without its antagonist, and the eyeball is immovable, as far as the twisting of the globe, just described, is concerned. When the head is moved toward the shoulder, the globe cannot rotate to maintain a position corresponding to that of the other eye, and we have double vision. This point has already been touched upon in connection with the physiology of the nerves of the eyeball and the situation of corresponding points in the retina.

Associated Action of the Different Muscles of the Eyeball.—It is almost unnecessary to add, after the description just given of the actions of the individual muscles of the globe, that their contractions may be associated, so as to produce an infinite variety of movements. We have no consciousness, under ordinary circumstances, of the muscular action by which the globe is rotated and twisted in various directions, except that, by an effort of the will, we direct the visual line toward different objects. By a strong effort, we can make the eyes converge by contracting both internal recti, and some persons can produce extreme divergence by using both external recti; but this is abnormal.

In looking at distant objects, the axes of vision are practically parallel. When we look at near objects, the effort of accommodation is attended with the amount of convergence necessary to bring the visual axes to bear upon identical points. In looking around at different objects, we move the head more or less, rotating and twisting the globes in various directions. In the movements of the globes vertically, the axes are kept parallel, or at the proper angle, by the internal and external recti, and the superior and inferior recti upon the two sides act together. In rotating the globe from one side to the other, upon a vertical axis, the external rectus upon one side acts with the internal rectus upon the other. In the movements of torsion upon an antero-posterior axis, there must be an associated action of the oblique muscles and the recti. We quote from Longet the following, as illustrative of this combination of action:

"If the eyes be directed obliquely upward and to the left, the vertical meridians of the two eyes are parallel and inclined from left to right, for the left eye, outward, and for the right eye, inward. The movement of the left eye upward and to the left, or outward, necessitates a contraction of the superior rectus, the external rectus, and the inferior oblique muscles. As regards the right eye, also directed upward and to the left, that is to say, inward, this is moved by the simultaneous action of the superior rectus, the internal rectus, and the inferior oblique."

We have given the above quotation simply to illustrate a combination of action of three muscles for each eye, the only difference in binocular vision being that in one eye the external rectus is brought into play, while the internal rectus acts upon the opposite side. Reversing this action of the internal and external recti, we have the action which directs the pupil upward and to the right. If we substitute for the superior rectus and the inferior oblique, the inferior rectus and the superior oblique, we have the pupil directed downward, and either to the right or left, as the internal or external rectus upon either side is brought into action.

One important point, never to be lost sight of in our study of the associated action of the muscles of the globe, relates to the associated movements of the two eyes. We have already seen that perfect binocular vision is possible only when impressions are made upon exactly corresponding points in the retina of each eye. If one eye be deviated in the horizontal plane, the points no longer correspond, and there is double vision, the same as if two impressions were made upon one retina; for, when the impressions exactly correspond, the two retinæ act practically as a single organ. The same is true in deviation of the globe in the vertical plane. If we suppose, for the sake of argument, that the retina is square, it is evident that a torsion, or twisting of one globe upon an antero-posterior axis must be attended with an analogous movement of the other globe, in order to bring the visual rays to bear upon the corresponding points; in other words, the obliquity of the assumed square of the retina must be exactly the same for the two eyes, or the coincidence of the corresponding points would be disturbed and we should have double vision. When we clearly understand that deviation of one eye in the horizontal or the vertical plane disturbs the relation of the corresponding points, which is sufficiently easy of comprehension, and that a deviation from exact coincidence of action in torsion of the globes twists, as it were, the corresponding points, so that their relation is also disturbed, we can see that the varied movements of the globes, by the combined action of the recti and oblique muscles, must correspond for each eye, in the movements of torsion upon an antero-posterior axis, as well as in movements of rotation upon the horizontal or the vertical axis.

Parts for the Protection of the Eyeball.

The orbit, formed by the union of certain of the bones of the face, receives the eyeball, the ocular muscles, the muscle of the upper lid, blood-vessels, nerves, part of the lachrymal apparatus, and contains, also, a certain amount of adipose tissue, which latter never disappears, even in extreme marasmus. The bony walls of this cavity protect the globe and lodge the parts above enumerated. The internal, or nasal wall of the orbit projects considerably beyond the external wall, so that the extent of vision is far greater in the outward than in the inward direction. As the globe is more exposed to accidental injury from an outward direction, the external wall of the orbit is strong, while the bones which form its internal wall are comparatively fragile. The upper border of the orbit (the superciliary ridge) is provided with short, stiff hairs (the eyebrows) which serve to shade the eye from excessive light and to protect the eyelids from perspiration from the forehead.

The eyelids are covered by a very thin integument and are lined by the conjunctival mucous membrane. The subcutaneous connective tissue is thin and loose and is entirely free from fat. The skin presents numerous short papillæ and small sudoriparous glands. At the borders of the lids, are short, stiff, curved hairs, arranged in two or more rows, called the eyelashes or cilia. Those of the upper lid are longer and more numerous than the lower cilia. The curve of the lashes is from the eyeball. They serve to protect the globe from dust, and, to a certain extent, to shade the eye.

The tarsal cartilages are small, elongated, semilunar plates, extending from the edges of the lids toward the margin of the orbit, between the skin and the mucous membrane. Their length is about an inch. The central portion of the upper cartilage is about one-third of an inch broad, and the corresponding part of the lower cartilage measures about one-sixth of an inch. At the inner canthus, or angle of the eye, is a small, delicate ligament, or tendon, the tendo palpebrarum, which is attached to the lachrymal groove internally, passes outward, and divides into two lamellæ, which are attached to the two tarsal cartilages. At the outer canthus, the cartilages are attached to the malar bone by the external tarsal ligament. The tarsal cartilages receive additional support from the palpebral ligament, a fibrous membrane attached to the margin of the orbit and the convex border of the cartilages and lying beneath the orbicularis muscle. This membrane is strongest near the outer angle of the eye.

On the posterior surface of the tarsal cartilages, partly embedded in them and lying just beneath the conjunctiva, are the Meibomian glands. The structure and functions of these glands have already been considered in connection with secretion. They produce an oily fluid, which smears the edges of the eyelids and prevents the overflow of tears.

Muscles which open and close the Eyelids.—Leaving out the corrugator supercilii, which draws the skin of the forehead downward and inward, we have the orbicularis palpebrarum, which closes the lids, and the levator palpebræ superioris, which raises the upper lid. The tensor tarsi, called the muscle of Horner, is a very thin, delicate muscle, which is regarded by some anatomists as a deep portion of the orbicularis. Considering this as a distinct muscle, it consists of two delicate slips, which pass from either eyelid behind the lachrymal sac, uniting here to go to its attachment at the posterior portion of the lachrymal bone. When this acts with the orbicularis, it compresses the lachrymal sac.

The orbicularis palpebrarum is a broad, thin muscle, closely attached to the skin, surrounding the free margin of the lids, and extending a short distance over the bones, beyond the margin of the orbit. This muscle may be described as arising from the tendo palpebrarum, the surface of the nasal process of the superior maxiliary bone, and the internal angular process of the os frontis. From this origin at the inner angle of the eye, its fibres pass elliptically around the fissure of the lids, as above indicated. Its action is to close the lids. In the ordinary, moderate contraction of this muscle, only the upper lid is moved; but, in forcible contraction, the lower lid moves slightly and the lids are drawn toward the nose. In facial palsy, or when the temporo-facial branch of the portio dura of the seventh nerve is paralyzed, this muscle cannot act, and it is impossible to close the eye.

The levator palpebræ superioris is situated within the orbit. It arises from a point a little above and in front of the optic foramen at the apex of the orbit, passes forward above the eyeball, and spreads into a thin tendon, which is inserted into the anterior surface of the superior tarsal cartilage. Its evident action is to raise the upper lid. It is animated by filaments from the third pair of cranial nerves; and, when this nerve is paralyzed, we have permanent falling of the upper lid, or blepharoptosis. This muscle and its relations are shown in Fig. 254 (9, 10, 10'), page 808.

In the act of opening the eyes, the levator muscles alone are brought into play. Closing of the lids is accomplished by the orbicular muscles. Both of these sets of muscles act to a great extent without the intervention of the will. The eyes are kept open almost involuntarily, except in extreme fatigue; although, when the will ceases to act, the lids are closed. Nevertheless, we are hardly conscious of an effort in keeping the eyes open, in our waking moments, and we require an effort to close the eyes. During sleep, the eyes are closed and the globes are turned upward. The contractions of the orbicular muscles which take place in winking are usually involuntary. This act occurs at short intervals, and it is useful in spreading the lachrymal secretion over the exposed portions of the globes. The action of both sets of muscles is usually simultaneous, although we may educate them so as to close one eye while the other is kept open. The action of the orbicularis is so far removed from the control of the will, that, when the surface of the globe is touched or irritated or when the impression of light produces intense pain, it is impossible to keep the eye open.

Conjunctival Mucous Membrane.—The entire inner surface of the upper and lower eyelids is lined by a mucous membrane, which is reflected forward from the inner periphery of the lids over the eyeball. The membrane lining the lids is called the palpebral conjunctiva, and that covering the eyeball, the ocular conjunctiva. The latter presents a sclerotic and a corneal portion. The membrane presents a superior and an inferior fold, where it is reflected upon the globe. In the superior conjunctival fold, are numerous glandular follicles, or accessory lachrymal glands, which secrete a certain portion of the fluid which moistens the surface of the eyeball. These are generally described as forming a part of the lachrymal gland. At the inner canthus, there is a vertical fold (the plica semilunaris) with a reddish, spongy elevation at its inner portion, called the caruncula lacrymalis. The caruncula presents a collection of follicular glands, with a few delicate hairs on its surface. The conjunctiva is continuous with the membrane of the lachrymal ducts, of the puncta lacrymalia, and of the Meibomian glands. Beneath the conjunctiva, except in the corneal portion, is a loose connective tissue.

The palpebral conjunctiva is reddish, thicker than the ocular portion, furrowed, and presents small, isolated papillæ near the borders of the lids, which increase in number and size toward the folds. This portion of the membrane presents large capillary blood-vessels and lymphatics and is covered with a layer of cells of flattened epithelium. The sclerotic portion is thinner, less vascular, and has no papillæ. It is covered by conical and rounded epithelial cells, which present from two to four layers. Over the cornea, the epithelium of the sclerotic portion is continued in delicate, transparent layers, without a distinct basement-membrane.

The Lachrymal Apparatus.—The eyeball is constantly bathed in a thin, watery fluid which is secreted by the lachrymal gland, is spread over the globe by the movements of the lids and of the eyeball, and is prevented, under ordinary conditions, from overflowing upon the cheek, by the Meibomian secretion. The excess of this fluid is collected into the lachrymal sac and is carried into the nose by the nasal duct. The lachrymal gland, the lachrymal canals, duct, and sac, and the nasal duct, constitute the lachrymal apparatus.

The lachrymal gland is an ovoid, flattened gland of the racemose variety, resembling the salivary glands in its general structure. It is about the size of a small almond and is lodged in a shallow depression in the bones of the orbit at its upper and outer portion. It is closely attached to the periosteum by its upper surface and is moulded below to the convexity of the globe. Its anterior portion is separated from the rest by a well-marked groove, is comparatively thin, and adheres to the upper lid. It presents from six to eight (usually seven) ducts, which form a row of openings into the conjunctival fold. Five or six of these orifices are situated above the outer canthus and two or three open below. In its minute structure, this gland presents no points of special physiological interest as distinguished from the ordinary racemose glands. It receives nervous filaments from the fifth cranial nerve and the sympathetic.

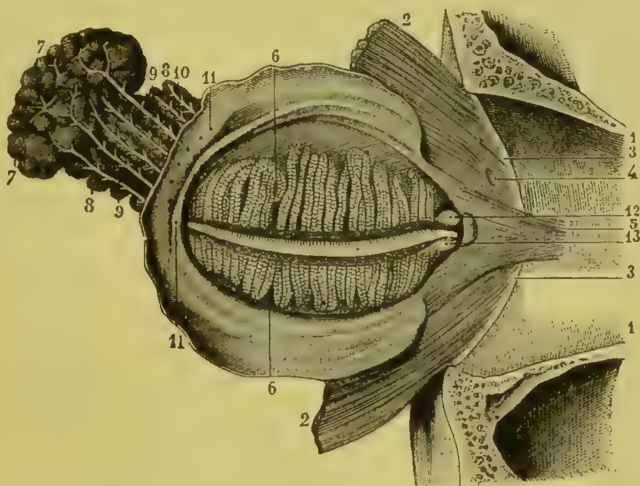


FIG. 256.—*Lachrymal and Meibomian glands.* (Sappey.)
1, 1, internal wall of the orbit; 2, 2, internal portion of the orbicularis palpebrarum; 3, 3, attachment of this muscle to the orbit; 4, orifice for the passage of the nasal artery; 5, muscle of Horner; 6, 6, posterior surface of the eyelids, with the Meibomian glands; 7, 7, 8, 8, 9, 9, 10, lachrymal gland and ducts; 11, openings of the lachrymal ducts.

The apparatus by which the excess of tears is conducted into the nose begins by two little points, situated on the margin of the upper and the lower lid, near the inner canthus, called the puncta lacrymalia, which present each a minute orifice. These orifices open respectively into the upper and the lower lachrymal canals, which together surround the caruncula lacrymalis. At the inner angle, just beyond the caruncula, the two canals join, to empty into the lachrymal sac, which is the dilated upper extremity of the nasal duct. The duct is about half an inch in length and empties into the inferior meatus of the nose, taking a direction nearly vertical, and inclined slightly outward and backward. This portion of the lachrymal apparatus is fibrous and is lined by a reddish mucous membrane, which presents several well-marked folds. Near the puncta, are two folds, one for each lachrymal canal. Another pair of folds exists near the horizontal portions of the canals. At the opening of the duct into the nose, is an overhanging fold of the nasal mucous membrane. These folds are supposed to prevent the reflux of fluid from the lachrymal canals and the entrance of air from the nose. The mucous membrane of the lachrymal canals is covered by a flattened epithelium, like that of the conjunctiva. The lachrymal sac and duct are lined by a continuation of the ciliated epithelium of the nose. The disposition of the apparatus just described is shown in Fig. 257.

The Tears.—The secretion of the lachrymal glands is constant, although the quantity of fluid may be increased under various conditions. The actual amount of the secretion has never been estimated. During sleep it is much diminished; and, when the eyes are open, the quantity is just sufficient to moisten the eyeball, the excess being carried into the nose so gradually that this process is not appreciated. That this drainage of the excess of tears takes place is shown by cases of obstruction of the nasal duct, when the liquid constantly overflows upon the cheeks, producing considerable inconvenience.

Fig. 257.—*Lachrymal canals, lachrymal sac, and nasal canal, opened by their anterior portion.* (Sappey.) 1, walls of the lachrymal passages, smooth and adherent; 2, 2, walls of the lachrymal sac, presenting delicate folds of the mucous membrane; 3, a similar fold belonging to the nasal mucous membrane.

The mechanism of the action of the excretory lachrymal apparatus is quite simple, though it has been the subject of a good deal of discussion. It is probable that the openings at the puncta lacrymalia take up the liquid like delicate pipettes, this action being aided by the movements in winking, by which, when the lids are closed, the points are compressed and turned backward, opening and drawing in the tears when the lids are opened. It is possible that the lachrymal sac is compressed in the act of winking, by the contractions of the muscle of Horner, and that this, while it empties the sac, may, in the subsequent relaxation, assist the introduction of liquid from the orbit.

We know very little with regard to the chemical composition of the tears, beyond the analysis made many years ago by Frerichs. According to this observer, the following is the composition of the lachrymal secretion:

Composition of the Tears.

Water	990·60	to	987·00
Epithelium	1·40	"	3·20
Albumen	0·80	"	1·00
Chloride of sodium, Alkaline phosphates, Earthy phosphates, Mucus, Fat,	7·20	"	8·80
	1,000·00		1,000·00

The specific gravity of the tears has never been ascertained. The liquid is perfectly clear, colorless, of a saltish taste and a feebly alkaline reaction. The albumen given in the table is called by some authors, lachrymine, thrænine, or dacryoline. This substance, whatever it may be called, resembles mucus in many regards and is probably secreted by the conjunctiva and not by the lachrymal glands. It differs from ordinary mucus in being coagulated by water.

The secretion of tears is readily influenced through the nervous system. Aside from the increased flow of this secretion from emotional causes, which probably operate through the sympathetic, a hypersecretion almost immediately follows irritation of the mucous membrane of the conjunctiva or of the nose. The same result follows violent muscular effort, laughing, coughing, sneezing, etc. The secretion of tears under stimulation of the mucous membrane is reflex.

CHAPTER XXV.

AUDITION.

Physiological anatomy of the auditory nerves—General properties of the auditory nerves—Topographical anatomy of the parts essential to the appreciation of sound—The external ear—General arrangement of the parts composing the middle ear—Anatomy of the tympanum—Arrangement of the ossicles of the ear—Muscles of the middle ear—Mastoid cells—Eustachian tube—Muscles of the Eustachian tube—Mucous membrane of the middle ear and of the Eustachian tube—General arrangement of the bony labyrinth—Laws of sonorous vibrations—Noise and musical sounds—Intensity, pitch, and quality of musical sounds—Musical scale—Harmonics, or overtones—Resonators of Helmholtz—Resultant tones—Summation tones—Harmony—Discord—Tones by influence (consonance)—Uses of different parts of the auditory apparatus—Uses of the external ear—Structure of the membrana tympani—Uses of the membrana tympani—Vibrations of the membrane by influence—Appreciation of the pitch of tones—Mechanism of the ossicles of the ear—Physiological anatomy of the internal ear—General arrangement of the membranous labyrinth—Vestibule—Semicircular canals—Cochlea—Liquids of the labyrinth—Distribution of nerves in the cochlea—Organ of Corti—Functions of different parts of the internal ear—Functions of the semicircular canals—Functions of the parts contained in the cochlea—Summary of the mechanism of audition.

The general considerations introductory to the study of vision are equally applicable to the physiology of hearing. The impressions of sound are conveyed to the brain by special nerves; but, in order that these impressions shall reach these nerves so as to be properly appreciated, a complex accessory apparatus is required, the integrity of which is essential to perfect audition. The study of the arrangement and action of these accessory parts is even more important and is far more intricate than the physiology of the auditory nerves. The latter simply convey the impressions to the brain, by a mechanism analogous to that of general nervous conduction, the essential character of which is not fully understood. The auditory nerves conduct impressions of sound, as the optic nerves conduct impressions of light; and this statement expresses the extent of our positive knowledge; but there is an elaborate apparatus by which the waves are collected, conveyed to a membrane capable of vibration, and finally carried to the nerves, by which we are enabled to appreciate the intensity and the varied qualities of sound.

Our positive and definite knowledge of the structure and arrangement of the auditory apparatus is by no means so complete as it is with regard to the eye, nor do we as yet understand so clearly the physiological relations of many points developed by late anatomical researches; and, for this reason, it does not seem desirable to consider the structure of the ear as fully as we have the anatomy of the eye, restricting ourselves, as we have done, to the physiological anatomy of parts. With this end in view, we shall take up fully the following points:

1. The physiological anatomy and the general properties of the auditory nerves.
2. The physiological anatomy of the parts essential to the correct appreciation of sound.
3. The laws of the propagation of sonorous vibrations, as far as they are applicable to audition.
4. The physiological action of different parts of the auditory apparatus.

Physiological Anatomy of the Auditory Nerves.—The auditory nerve constitutes the portio mollis of the seventh pair of Willis. The origin of this nerve can easily be traced to the floor of the fourth ventricle, where it presents two roots. The external, or superficial root, sometimes called the posterior root, can be seen usually without preparation. This consists of from five to seven grayish filaments, which decussate in the median line, and pass outward, winding from the fourth ventricle around the restiform body. The deep root consists of numerous distinct filaments, arising from the gray matter of the fourth ventricle, two or three of which pass to the median line to decussate with corresponding filaments from the opposite side. This root passes around the restiform body inward, so that this portion of the medulla is encircled, as it were, by the two roots. Passing from the superior and lateral portion of the medulla oblongata, the trunk of the nerve is applied to the superior and anterior surface of the facial. It then passes around the middle peduncle of the cerebellum, and receives a process from the arachnoid membrane, which envelops it in a common sheath with the facial. It then penetrates the internal auditory meatus. In its course, it receives filaments from the restiform body, and possibly from the pons Varolii. Within the meatus, the nerve divides into an anterior and a posterior branch, the anterior being distributed to the cochlea, and the posterior, to the vestibule and semicircular canals. The distribution of these branches will be fully described in connection with the anatomy of the internal ear.

The color of the auditory nerves is grayish, and their consistence is soft, thus differing from the ordinary cerebro-spinal nerves, and resembling, to a certain extent, the other nerves of special sense. On the external, or superficial root, is a small ganglioform enlargement, containing fusiform nerve-cells. According to the latest researches, the filaments of the trunk of this nerve consist of very large axis-cylinders, surrounded by a medullary sheath, but having no tubular membrane. In the course of these fibres, are found small, nucleated ganglionic enlargements.

General Properties of the Auditory Nerves.—There can be no doubt, as regards the portio mollis of the seventh, that it is the only nerve capable of receiving and conveying to the brain the special impressions produced by waves of sound; but it is an interesting question to determine, whether this nerve be endowed also with general sensibility. Analogy with most of the other nerves of special sense would indicate that the auditory nerves are insensible to ordinary impressions; and this view is sustained by direct experiments, made many years ago.

The phenomena observed during the passage of galvanic currents through the auditory nerves have, of late years, been the subject of much discussion. The old experiment of Volta, which was almost immediately confirmed by Ritter, is sufficiently familiar and is often quoted as showing that galvanic stimulation of these nerves produces a sensation of sound; but the facts ascertained leave room for doubt with regard to the precise mode of action of the current. A careful study of recent observations upon this point renders the question even more obscure; but, from a purely physiological point of view, we have only to do with the effects of stimulating the auditory nerves in health. Leaving the therapeutic and diagnostic uses of galvanism out of the question, we find that there is considerable uncertainty with regard to the fact of direct stimulation of the auditory nerves, in the recent experiments with the galvanic current. Brenner observed strong sensations of sound with one of the poles of a battery in the auditory passage filled with water and the other connected with different parts of the body. When the cathode was placed in the ear, the sound was heard at the making of the current. With the anode in the ear, there was no sound at the making of the current or during its passage, but a slight sound was heard at the breaking of the current. These phenomena closely resemble those produced by the galvanic current applied to ordinary motor nerves, in so far as the action seemed to be most vigorous at the making of the circuit, with the direct current, and at the breaking of the circuit, with the inverse current; for, when the cathode is placed in the ear, the current is direct, following the course of the nerve from the centre to the periphery, and *vice versa*. Without following out the discussion of this question in detail, it seems only necessary to study the very clear and satisfactory experiments of Wreden, to become convinced that the subjective auditory phenomena, attributed by Brenner and others to irritation of the auditory nerves, are due to contraction of the muscles of the middle ear, particularly the stapedius. The facts, clinical and experimental, upon which this view is based, are the following: In cases of clonic spasm of the stapedius, sensations of sound have been observed, exactly like those produced by an induced current. In cases of complete facial paralysis from otitis, in which paralysis of the auditory nerve could be positively excluded, it was not possible to produce subjective auditory sensations, even by powerful galvanization by a catheter passed through the Eustachian tube into the tympanic cavity, or by the external meatus. In addition, there are other well-established clinical observations, mentioned by Wreden, which sustain the theory of muscular contraction and are opposed to the idea of direct stimulation of the auditory nerves.

The facts just stated show that there is no positive evidence of the production of impressions of sound by galvanic stimulation of the auditory nerves; while it appears from experiments, that these nerves are not endowed with general sensibility. The results, then, as regards the auditory nerves, are simply negative. Were it possible to subject these nerves to mechanical or galvanic stimulation, in the human subject, without involving other parts, we might arrive at some definite conclusion; but the difficulties in the way of such an experiment, it must be admitted, have thus far proved insurmountable.

Topographical Anatomy of the Parts essential to the Appreciation of Sound.

Perfect audition requires the anatomical integrity of a very complex apparatus, which, for convenience of anatomical description, may be divided into the external, middle, and internal ear. A correct appreciation of the physiology of these parts demands, as a necessary preparation, a knowledge of their physiological anatomy:

1. The external ear includes the pinna and the external auditory meatus, which is closed internally by the membrana tympani.

2. The middle ear includes the cavity of the tympanum, or drum, with its boundaries. The parts here to be described are, the membrana tympani, the form of the tympanic cavity, its openings, its lining membrane, and the small bones of the ear, or ossicles, with their ligaments, muscles, and nerves. The cavity of the tympanum communicates, by the Eustachian tube, with the pharynx and also presents openings into the mastoid cells.

3. The internal ear contains the terminal filaments of the auditory nerve. It includes the vestibule, the three semicircular canals, and the cochlea, which together form the labyrinth.

The pinna and the external meatus simply conduct the waves of sound to the tympanum. The parts entering into the structure of the middle ear are accessory, and are analogous in their functions to the refracting media of the eye. Structures contained in the labyrinth constitute the true sensory organ; and these bear the same relations to the auditory apparatus as the retina to the eye.

The External Ear.—It is hardly necessary to our purpose to describe very minutely the external ear. The pinna, or auricle is that portion projecting from the head, which first receives the waves of sound. Beginning externally, we have the helix, which is the outer ridge of the pinna. Just within this, is a groove, called the fossa of the helix. This fossa is bounded anteriorly by a prominent but shorter ridge, called the antihelix; and above the concha, between the superior portion of the antihelix and the anterior portion of the helix, is a shallow fossa, called the fossa of the antihelix. The deep fossa, immediately surrounding the opening of the meatus, is called the concha. A small lobe projects posteriorly, covering the anterior portion of the concha, which is called the tragus; and the projection at the lower extremity of the antihelix is called the antitragus. The fleshy, dependent portion of the pinna is called the lobule of the ear.

The form of the pinna and its consistence depend upon the presence of fibro-cartilage, which occupies the whole of the external ear except the lobule. This structure has already been described in another chapter.

The integument covering the ear does not vary much from the integument of the general surface. It is thin, closely attached to the subjacent parts, and possesses small, rudimentary hairs, with sudoriparous and sebaceous glands.

The muscles of the ear are not important in the human subject; and, excluding a few exceptional cases, they are not under the control of the will. The extrinsic muscles are the superior, or attollens, the anterior, or attrahens, and the posterior, or retrahens aurem. In addition, there are the six small intrinsic muscles, situated between the ridges upon the cartilaginous surface. The pinna is attached to the sides of the head by two distinct ligaments and a few delicate ligamentous fibres.

The external auditory meatus is about an inch and a quarter in length and extends from the concha to the membrana tympani. Its course is somewhat tortuous. Passing from without inward, its direction is at first somewhat upward, turning abruptly over a bony prominence near the middle, from which it has a slightly downward direction to the membrana tympani. Its general course is from without inward and slightly forward. The inner termination of the canal is the membrana tympani, which is quite oblique, the upper portion being inclined outward, so that the inferior wall of the meatus is considerably longer than the superior.

The walls of the external meatus are partly cartilaginous and fibrous, and partly bony. The cartilaginous and fibrous portion occupies a little less than one-half of the entire length and consists of a continuation of the cartilage of the pinna, with fibrous tissue. About the lower two-thirds of this portion of the canal is cartilaginous, the upper third being fibrous. The rest of the tube is osseous and is a little longer and narrower than the cartilaginous portion. Around the inner extremity of the canal, with the exception of its superior portion, is a narrow groove, which receives the greater portion of the margin of the membrana tympani.

The skin of the external meatus is continuous with the integument covering the pinna. It is very delicate, becoming thinner from without inward. In the osseous portion, it adheres very closely to the periosteum, and, at the bottom of the canal, it is reflected over the membrana tympani, forming its outer layer. In the cartilaginous and fibrous portion, are numerous short, stiff hairs, with sebaceous glands attached to their follicles, and the coiled tubes known as the ceruminous glands. The structure of these glands and the properties and composition of the cerumen have already been described under the head of secretion.

General Arrangement of the Parts composing the Middle Ear.—Without a very elaborate and minute anatomical description, fully illustrated by plates, it is difficult to give a clear idea of the structure and relations of the very complex apparatus of the middle and the internal ear. Such a minute and purely anatomical description would be out of place in this work, where it is desired only to give such an account of the anatomy as will enable the student to comprehend the physiology of the ear, reserving for special description certain of the most important structures. In beginning the difficult task of describing the physiological anatomy of the middle and internal ear, it will be convenient to give a general outline of the different parts, with their names. This, with a careful study of Figs. 258, 259, 260, and 261, can hardly fail to greatly facilitate the closer investigation of the more important structures.

The arrangement of the parts constituting the external ear is sufficiently simple. The middle ear presents a narrow cavity (Fig. 258, 11), of irregular shape, situated between the external ear and the labyrinth, in the substance of the temporal bone. The general arrangement of its parts is shown in Fig. 258. The outer wall of the tympanic cavity is formed by the membrana tympani (Fig. 258, 6). This membrane is concave, its concavity looking outward, and oblique, inclining usually at an angle of forty-five degrees with the perpendicular. This angle, however, varies considerably in different individuals. The roof is formed by an exceedingly thin plate of bone. The floor is bony and is much narrower than the roof. The inner wall, separating the tympanic cavity from the labyrinth, is irregular, presenting several small elevations and foramina. The fenestra ovalis, an ovoid opening near its upper portion, leads to the cavity of the vestibule. This is

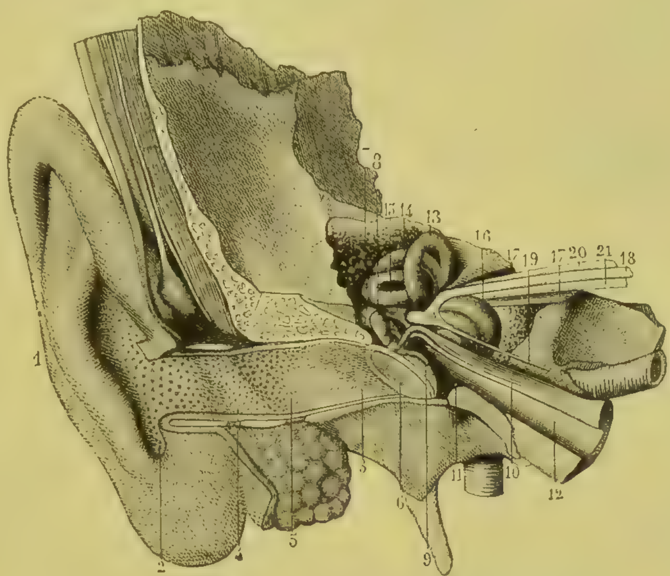


FIG. 258.—*General view of the organ of hearing.* (Sappey.)

1, pinna; 2, cavity of the concha, on the walls of which are seen the orifices of a great number of sebaceous glands; 3, external auditory meatus; 4, angular projection formed by the union of the anterior portion of the concha with the posterior wall of the auditory canal; 5, openings of the ceruminous glands, the most internal of which form a curved line which corresponds with the beginning of the osseous portion of the external meatus; 6, membrana tympani and the elastic fibrous membrane which forms its border; 7, anterior portion of the incus; 8, malleus; 9, handle of the malleus applied to the internal surface of the membrana tympani, which it draws inward toward the projection of the promontory; 10, tensor tympani muscle, the tendon of which is reflected at a right angle to become attached to the superior portion of the handle of the malleus; 11, tympanic cavity; 12, Eustachian tube, the internal, or pharyngeal extremity of which has been removed by a section perpendicular to its curve; 13, superior semicircular canal; 14, posterior semicircular canal; 15, external semicircular canal, 16, cochlea; 17, internal auditory canal; 18, facial nerve; 19, large petrosal branch, given off from the ganglioform enlargement of the facial and passing below the cochlea to go to its distribution; 20, vestibular branch of the auditory nerve; 21, cochlear branch of the auditory nerve.

closed, in the natural state, by the base of the stapes and its annular ligament. Below, is a smaller, ovoid opening, the fenestra rotunda, which leads to the cochlea. This is closed, in the natural state, by a membrane, called the secondary membrana tympani. In addition, the posterior wall presents several small foramina leading to the mastoid cells, which are lined by a continuation of the mucous membrane of the tympanic cavity. The tympanic cavity also presents an opening leading to the Eustachian tube, and a small foramen, which gives passage to the tendon of the stapedius muscle. The Eustachian tube extends from the upper part of the pharynx to the tympanum.

The small bones of the ear are three in number; the incus, the malleus, and the stapes, forming a chain, connected together by ligaments (Fig. 259). These bones are situated in the upper part of the tympanic cavity. The handle of the malleus (A, 2, Fig. 259) is closely attached to the membrana tympani, and the long process (A, 3, Fig. 259) is attached to the Glasserian fissure of the temporal bone. The malleus is articulated with the incus. The incus (B, Fig. 259) is connected with the posterior wall of the tympanic cavity, near the openings of the mastoid cells. It is articulated with the malleus, and, by the extremity of its long process (B, 2, Fig. 259), with the stapes. The stapes (C, Fig. 259) is the most internal bone of the middle ear. It is articulated by its smaller extremity with the long process of the incus. Its base is oval (C*, Fig. 259) and, with its annular ligament, is applied to the fenestra ovalis. The direction of the stapes is nearly at a right angle with the long process of the incus in the natural state (8, Fig. 260).

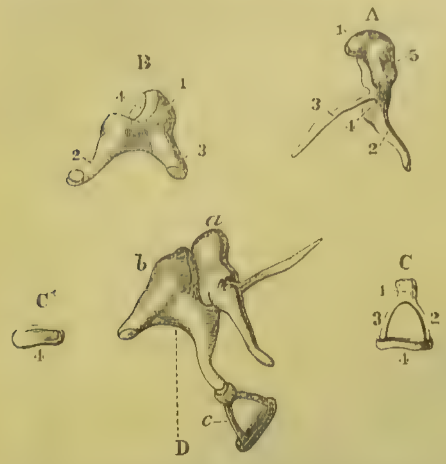


FIG. 259.—*Ossicles of the tympanum of the right side; magnified 2 diameters.* (Arnold.)

A, malleus; 1, its head; 2, the handle; 3, long, or slender process; 4, short process; B, incus; 1, its body; 2, the long process with the orbicular process; 3, short, or posterior process; 4, articular surface receiving the head of the malleus; C, stapes; 1, head; 2, posterior crus; 3, anterior crus; 4, base; C*, base of the stapes; D, the three bones in their natural connection as seen from the outside; *a*, malleus; *b*, incus; *c*, stapes.

There are three well-defined muscles connected with the middle ear. Of these, two are attached to the malleus, and one, to the stapes.

The largest of the three muscles is the tensor tympani, called sometimes the internal muscle of the malleus. Its fibres arise from the cartilaginous portion of the Eustachian tube, the spinous process of the sphenoid bone, and the adjacent portion of the temporal. From this origin, it passes backward, almost horizontally, to the tympanic cavity. In front of the fenestra ovalis, it turns, nearly at a right angle, over a bony process, and its tendon is inserted into the handle of the malleus at its inner surface near the root. The tendon is very delicate, and the muscular portion is about half an inch in length (10, Fig. 258). The muscle and its tendon are enclosed in a distinct fibrous sheath. The action of this muscle is to draw the handle of the malleus inward, pressing the base of the stapes against the membrane of the fenestra ovalis and producing tension of the membrana tympani. The fibres of this, and of all the muscles of the middle ear, are of the striated variety. The tensor tympani is supplied with motor filaments from the otic ganglion, which are probably derived from the facial nerve.

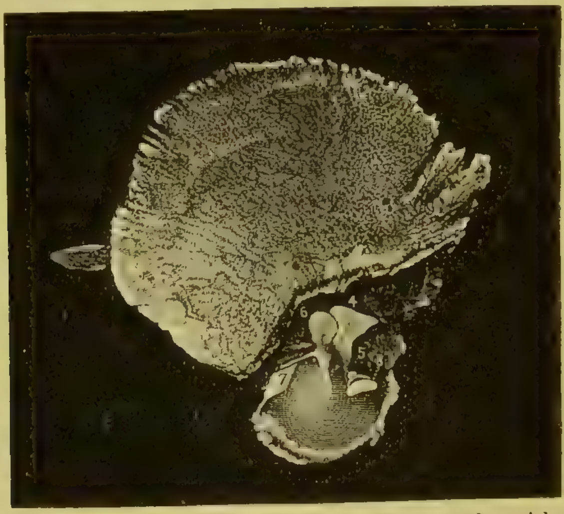


FIG. 260.—*The right temporal bone, the petrosal portion removed, showing the ossicles seen from within.* From a photograph. (Rüdinger.)

4, the incus, the short process of which is directed nearly in an horizontal direction backward; 5, the long process of the incus, free in the tympanic cavity, articulated with the stapes; 6, the malleus, articulated with the incus; 7, the long process of the malleus in the Glasserian fissure; 8, the stapes, articulated with the incus. This is drawn somewhat outward; otherwise, the base of the stapes alone would be visible. This figure shows the handle of the malleus attached to the membrana tympani.

The laxator tympani, the external muscle of the malleus, arises from the spinous process of the sphenoid bone and, by a few filaments, from the cartilaginous portion of the

Eustachian tube. It passes backward, through the Glasserian fissure, to be inserted into the neck of the malleus, being enclosed, in its course, in a fibrous sheath. The laxator tympani is generally believed to be muscular, though some authorities deny that it is composed of true muscular fibres. Its action would be to draw the malleus forward and outward, producing relaxation of the membrana tympani. It is not definitely known from what nerve this muscle derives its motor filaments.

The stapedius muscle is situated in the descending portion of the aqueductus Fallopii and in the cavity of the pyramid on the posterior wall of the tympanic cavity. Its tendon emerges from a foramen at the summit of the pyramid. In the canal in which this muscle is lodged, its direction is upward and vertical. At the summit of the pyramid, it turns at nearly a right angle, its tendon passing horizontally forward to be attached to the head of the stapes. Like the other muscles of the ear, this is enveloped in a fibrous sheath. Its action is to draw the head of the stapes backward, relaxing the membrana tympani. This muscle receives filaments from the facial nerve by a distinct branch, the tympanic.

The posterior wall of the tympanic cavity presents several foramina which open directly into numerous irregularly-shaped cavities, communicating freely with each other, in the mastoid process of the temporal bone. These are called the mastoid cells. They are lined by a continuation of the mucous membrane of the tympanum. There is, under certain conditions, a free circulation of air between the pharynx and the cavity of the tympanum through the Eustachian tube, and from the tympanum to the mastoid cells.

The Eustachian tube (12, Fig. 258) is partly bony and partly cartilaginous. Following its direction from the tympanic cavity, it passes forward, inward, and slightly downward. Its entire length is about an inch and a half. Its caliber gradually contracts from the tympanum to the spine of the sphenoid, and from this constricted portion it gradually dilates to its opening into the pharynx, the entire canal presenting the appearance of two cones. The osseous portion extends from the tympanum to the spine of the sphenoid bone. The cartilaginous portion is an irregularly triangular cartilage, bent upon itself above, forming a furrow, with its concavity presenting downward and outward. The fibrous portion occupies about half of the tube beyond the osseous portion, and completes the canal, forming its inferior and external portion. In its structure, the cartilage of the Eustachian tube is intermediate between the hyaline and the fibro-cartilage.

The circumflexus, or tensor palati muscle, which has already been described in connection with deglutition, is attached to the anterior margin, or the hook of the cartilage. The attachments of this muscle have lately been accurately described by Rüdinger, who calls it the dilator of the tube. The following excellent summary of the action of the muscles upon the tube is taken from the report on otology, by Dr. J. Orne Green, contained in the Transactions of the American Otological Society, 1870:

"The tensor palati muscle is a dilator of the tube; it is inserted along the whole length of the hook of the cartilage, passing forward, inward, and slightly downward, and its fibres spread out along the edge of the soft palate and on the side of the pharynx. In contracting, it draws the hook of the cartilage forward and a little downward, thus enlarging the caliber of the tube. The levator palati takes its origin from the temporal bone just below the osseous tube, and passes along the floor of the tube, some of its fibres arising from the lower end of the cartilage; it is inserted in the uvula, and, in contracting the belly of the muscle which lies along the floor of the tube, becomes thicker: the floor of the tube is raised, and the fibres arising from the cartilage serve to draw the lower end of this away from the opposite wall.

"The palato-pharyngeus rises from the posterior part of the lower end of the cartilage, passes backward, and is inserted on the posterior wall of the pharynx. Its action would be to draw the posterior wall of the tube backward; but, as it is often but slightly developed, it probably only serves to fix the cartilage, so that the other muscles can act more effectively.

"The opening of the tube is thus the result of the action of these three muscles: the tensor palati, or dilator tubæ, draws the hook of the cartilage outward, the cartilage becomes less curved and the tube is widened; the levator palati in contracting becomes more horizontal, and draws the lower end of the cartilage inward and upward, thus enlarging the pharyngeal orifice more than 3‴. As soon as these muscles cease acting, the elasticity of the cartilage restores the canal to its former condition."

It is thus that the action of certain of the muscles of deglutition dilates the pharyngeal opening of the Eustachian tube. If we close the mouth and nostrils and make several repeated acts of deglutition, we draw the air from the tympanic cavity, and the atmospheric pressure renders the membrane of the tympanum tense, increasing its concavity. By one or two lateral movements of the jaws, we open the tube, the pressure of air is equalized, and the ear returns to its normal condition. The nerves animating the dilator tubæ come from the pneumogastric and are derived from the spinal accessory.

A smooth mucous membrane forms a continuous lining for the Eustachian tube, the cavity of the tympanum, and the mastoid cells. In all parts, it is closely adherent to the subjacent tissues, and, in the cavity of the tympanum, it is very thin. In the cartilaginous portion of the Eustachian tube, there are numerous mucous glands, which are most abundant near the pharyngeal orifice, and gradually diminish in number toward the osseous portion, in which there are no glands. Throughout the tube, the surface of the mucous membrane is covered with conoidal cells of ciliated epithelium. The mucous membrane of the tympanic cavity is very thin, consisting of little more than epithelium and a layer of connective tissue. It lines the walls of the cavity, the inner surface of the membrana tympani, is prolonged into the mastoid cells, and covers the ossicles and those portions of the muscles and tendons which pass through the tympanum. On the floor of the tympanic cavity and on its anterior, inner, and posterior walls, the epithelium is of the conoidal, ciliated variety. On the promontory, roof, ossicles, and muscles, the cells are of the pavement-variety and not ciliated, the transition from one form to the other being gradual. The entire mucous membrane contains numerous lymphatics, a plexus of nerve-fibres and nerve-cells, with some peculiar cells, the physiology of which is not understood.

We have thus given a general sketch of the physiological anatomy of the middle ear, and shall not find it necessary to treat more fully of the cavity of the tympanum, the mastoid cells, or the Eustachian tube, except as regards certain points in their physiology. The minute anatomy of the membrana tympani and the articulations of the ossicles can be more conveniently considered in connection with the physiology of these parts.

General Arrangement of the Bony Labyrinth.—The internal portion of the auditory apparatus is contained in the petrous portion of the temporal bone. It consists of an irregular cavity, called the vestibule, the three semicircular canals (13, 14, 15, Fig. 258), and the cochlea (16, Fig. 258). The general arrangement of these parts *in situ* and their relations to the adjacent structures are shown in Fig. 258. Fig. 261, showing the bony labyrinth isolated, is taken from the beautiful photograph contained in Rüdinger's atlas.

The vestibule is the central chamber of the labyrinth, communicating with the tympanic cavity by the fenestra ovalis, which is closed in the natural state by the base of the stapes. This is the central, ovoid opening shown in Fig. 261. The inner wall of the vestibule presents a small, round depression (the fovea hemispherica) perforated by numerous small foramina, through which pass nervous filaments from the internal auditory meatus. Behind this depression, is the opening of the aqueduct of the vestibule. In the posterior wall of the vestibule, are five small, round openings leading to the semicircular canals, with a larger opening below, leading to the cochlea.

The general arrangement of the semicircular canals is shown in Fig. 261 (6, 7, 8, 9, 10, 11, 12).

The arrangement of the cochlea (the anterior division of the labyrinth) is shown in

Fig. 261 (1, 3, 4). This is a spiral canal, about an inch and a half long, and one-tenth of an inch wide at its commencement, gradually tapering to the apex, and making, in its course, two and a half turns. Its interior presents a central pillar, around which winds a spiral lamina of bone. The fenestra rotunda (2, Fig. 261), closed in the natural state by a membrane (the secondary membrana tympani), lies between the lower portion of the cochlea and the cavity of the tympanum.

FIG. 261.—*The left bony labyrinth of a new-born child, forward and outward view.* From a photograph. (Rüdinger.)

1, the wide canal, the beginning of the spiral canal of the cochlea; 2, the fenestra rotunda; 3, the second turn of the cochlea; 4, the final half-turn of the cochlea; 5, the border of the bony wall of the vestibule, situated between the cochlea and the semicircular canals; 6, the superior, or sagittal semicircular canal; 7, the portion of the superior semicircular canal bent outward; 8, the posterior, or transverse semicircular canal; 9, the portion of the posterior connected with the superior semicircular canal; 10, point of junction of the superior and the posterior semicircular canal; 11, the ampulla ossea externa; 12, the horizontal, or external semicircular canal. The explanation of this Figure has been modified and condensed from Rüdinger.

What is called the membranous labyrinth is contained within the bony parts just described. Its structure, and the ultimate distribution and connections of the auditory nerve, which penetrates by the internal auditory meatus, involve some of the most intricate and difficult points in the whole range of minute anatomy. Some of these have direct and important relations to the physiology of hearing, while many are of purely anatomical interest. Such facts as bear directly upon physiology will be considered fully in connection with the functions of the internal ear.

Physics of Sound.

The sketch that we have given of the general anatomical arrangement of the auditory apparatus conveys an idea of the uses of the different parts of the ear. The waves of sound must be transmitted to the terminal extremities of the auditory nerve in the labyrinth. These waves are collected by the pinna, are conducted to the membrana tympani through the external auditory meatus, produce vibrations of the membrana tympani, are conducted by the chain of ossicles to the openings in the labyrinth, and are communicated through the fluids of the labyrinth to the ultimate nervous filaments. The free passage of air through the external meatus and the communications of the cavity of the tympanum with the mastoid cells, and, by the Eustachian tube, with the pharynx, are necessary to the proper vibration of the membrana tympani; the integrity of the ossicles and of their ligaments and muscles is essential to the proper conduction of sound to the labyrinth; the presence of liquid in the labyrinth is a condition essential to the conduction of the waves to the filaments of distribution of the auditory nerves; and, finally, from the labyrinth, the nerves pass through the internal auditory meatus to the brain, where the auditory impressions are appreciated.

Most of the points in acoustics which are essential to the comprehension of the physiology of audition are definitely settled. The theories of the propagation of sound involve wave-action, concerning which there is no dispute among physicists. For the conduction of sound, a ponderable medium is essential; and it is not necessary, as in the case of the undulatory theory of light, to assume the existence of an imponderable ether. The human ear, although perhaps not so acute as the auditory apparatus of some of the inferior animals, not only appreciates irregular waves, such as produce noise as distinguished from sounds called musical, but is capable of distinguishing regular waves, as in simple musical sounds, and harmonious combinations.

In music, certain successions of regular sounds are agreeable to the ear and constitute what we call melody. Again, we are able to appreciate, not only the intensity of sounds, both noisy and musical, but we recognize pitch and different qualities, particularly in music. Still farther, we find that musical notes may be resolved into certain invariable component parts, such as the octave, the third, fifth, etc. These components of what are usually supposed to be simple sounds—which may be isolated by artificial means, to be described farther on—are called tones; while the sounds themselves, produced by the union of the different tones, are called notes, which may themselves be combined to form chords.

The quality of musical sounds may be modified by the simultaneous production of others which correspond to certain of the components of the predominating note. For example, if we add to a single note, the third, fifth, and octave, we produce a major chord, the sound of which is very different from that of a single note or of a note with its octave. If we diminish the third by a semitone, we have a different quality, which is peculiar to minor chords. In this way, we can form an immense variety of musical sounds upon a single instrument, as the piano. And still farther, by the harmonious combinations of the notes of different instruments and of different registers of the human voice, as in grand choral and orchestral compositions, shades of effect, almost innumerable, may be produced. The modification of tones in this way constitutes harmony; and an educated ear, not only experiences pleasure from these musical combinations, but can distinguish their different component parts.

A chord may convey to the ear the sensation of completeness in itself or it may lead to a succession of notes before this sense of completeness is attained. Different chords of the same key may be made to follow each other, or we may, by transition-notes, pass to the chords of other keys. Each key has its fundamental note, and the transition from one key to another, in order to be agreeable to the ear, must be made in certain well-defined and invariable ways. These regular transitions constitute modulation. The ear becomes fatigued by long successions of notes always in one key, and modulation is essential to the enjoyment of elaborate musical compositions; otherwise, the notes would not only become monotonous, but their correct appreciation would be impaired, as the appreciation of colors becomes less distinct after looking for a long time at an object presenting a single vivid tint.

Laws of Sonorous Vibrations.

As we have already remarked, sound is produced by vibrations in a ponderable medium. The sounds ordinarily heard are transmitted to the ear by means of vibrations of the atmosphere. A simple and very common illustration of this fact is afforded by the experiment of striking a bell carefully arranged *in vacuo*. Although the stroke and the vibration can readily be seen, there is no sound; and, if air be gradually introduced, the sound will become appreciable and progressively more intense as the surrounding medium is increased in density.

If we produce a single sound, or shock, in a free atmosphere, we may suppose that the waves are transmitted equally in every direction; and this is accomplished in the following manner: An imaginary sphere of air receives an impulse, or shock, from the body which produces the sound. This shock is, in its turn, communicated to another spherical stratum of air; this, to a third, and so on. The elasticity of the air, however, produces a recoil of each imaginary sphere of air, and it is a portion of the last stratum which strikes the tympanum, throwing it into vibration. If but a single impulse be given to the air, we may suppose that all of the different strata, after a single oscillation, return to their original quiescent condition. The first stratum receives the shock, and the last communicates the shock to the ear. The oscillations of sound, produced in this way, are to and fro in the direction of the line of conduction and are said to be longitudinal. In the undulatory theory of light, the vibrations are supposed to be at right angles to the line of propagation, or transversal. A complete oscillation to and fro is called a sound-wave.

It is evident that vibrating bodies may be made to perform and impart to the atmosphere oscillations of greater or less amplitude. The intensity of the sound is in proportion to the amplitude of the vibrations. If we cause a tuning-fork to vibrate, the sound is at first loud, or intense; but the amplitude gradually diminishes, and the sound dies away until it is lost. In a vibrating body capable of producing a definite number of waves of sound in a second, it is evident that, the greater the amplitude of the wave, the greater is the velocity of the particles thrown into vibration. It has been ascertained by experiment, that there is an invariable mathematical relation between the intensity of sound, the velocity of the conducting particles, and the amplitude of the waves; and this is expressed by the formula, that the intensity is proportional to the square of the amplitude. It is evident, also, that the intensity of sound is diminished by distance, as the amplitude of the waves and the velocity of the vibrating particles become weaker, the farther we are removed from the sonorous body. The sound, as the waves recede from the sonorous body, becomes distributed over an increased area. The propagation of sound has been reduced also to the formula, that the intensity diminishes in proportion to the square of the distance.

Sonorous vibrations are subject to many of the laws of reflection which we have studied in connection with light. Sound may be absorbed by soft and non-vibrating surfaces, in the same way that certain surfaces absorb the rays of light. It is in this way that we explain the deadening of sound in apartments furnished with carpets, curtains, etc., and its reflection from smooth, hard surfaces. By carefully-arranged convex surfaces, the waves of sound may be readily collected to a focus. These laws of the reflection of sonorous waves explain echoes and the conduction of sound by confined strata of air, as in tubes. We thus explain the mechanism of speaking-trumpets, the collection of the waves by the pavilion of the ear, and their transmission to the tympanum by the external auditory meatus. To make the parallel between sonorous and luminous transmission more complete, it has been ascertained that the waves of sound may be refracted to a focus by being made to pass through an acoustic lens, as a balloon filled with carbonic-acid gas. The waves of sound may also be deflected around solid bodies, when they produce what have been called by Tyndall, shadows of sound.

Any one observing the sound produced by the blow of an axe can note the important fact that sound is transmitted with much less rapidity than light. At a short distance, our view of the body is practically instantaneous; but there is a considerable interval between the blow and the sound. This interval represents the velocity of the sonorous conduction. This fact is also illustrated by the interval between a flash of lightning and the sound of thunder. The velocity of sound depends upon the density and elasticity of the conducting medium. The rate of conduction of sound by atmospheric air at the freezing-point of water is about 1,090 feet per second. This rate presents comparatively slight variations for the different gases, but it is very much more rapid in liquids and in solids. In ordinary water, it is 4,708 feet per second; in iron or steel wire, about 16,000 feet; and in most woods, in the direction of the fibre, about the same.

Noise and Musical Sounds.—There is a well-defined physical as well as an æsthetic distinction between noise and music. Taking, as examples, single sounds, a sound becomes noise when the air is thrown into confused and irregular vibrations. A noise may be composed of a few musical sounds, when these are not in accord with each other, and sounds called musical are not always entirely free from discordant vibrations, as we shall see in studying musical sounds, properly so called. A noise possesses intensity, varying with the amplitude of the vibrations, and it may have different qualities, depending upon the form of its vibrations. We may call a noise dull, sharp, ringing, metallic, hollow, etc., thus expressing qualities that are readily understood. In percussion of the chest, the resonance is called vesicular, tympanitic, etc., distinctions in quality that are quite important. A noise may also be called sharp or low in pitch, as the rapid or slow vibrations predominate, without answering the requirements of musical sounds. These explanations, with the definition that a noise is a sound that is not musical, will be better understood after we have described some of the characters of musical vibrations.

A pure and simple musical sound consists of vibrations following each other at regular intervals, provided that the succession of waves be not too slow or too rapid. When the vibrations are too slow, we have an appreciable succession of impulses, and the sound is not musical. When they are too rapid, we recognize that the sound is excessively sharp, but it is then painfully acute and has no pitch that can be accurately determined by the auditory apparatus. Such sounds may be occasionally employed in musical compositions, but, in themselves, they are not strictly musical.

In musical sounds, we recognize duration, intensity, pitch, and quality. The duration depends simply upon the length of time during which the vibrating body is thrown into action. The intensity depends, as we have already stated, upon the amplitude of the vibrations, and it has no relation whatsoever to pitch. Pitch depends absolutely upon the rapidity of the regular vibrations, and quality, upon the combinations of different tones in harmony, the character of the harmonics of fundamental tones, and the form of the vibrations.

Pitch of Musical Sounds.—In discussing the pitch of musical sounds, we shall leave out of the question, for the present, the harmonics, which exist in nearly all musical notes and affect their quality, and confine ourselves to the study of simple vibrations. Such tones are those of great organ-pipes, which are deficient in harmonics and in overtones, and are almost entirely pure.

Pitch depends upon the number of vibrations. A musical sound may be of greater or less intensity; it may at first be quite loud and gradually die away; but the number of vibrations in a definite tone is invariable, be it weak or powerful. The rapidity of the conduction of sound does not vary with its intensity or pitch, and, in the harmonious combination of the sounds of different instruments, be they high or low in pitch, intense or feeble, it is always the same in the same conducting medium. Distinct musical notes may present an immense variety of qualities, but all tones of the same pitch have absolutely equal rates of vibration. Tones equal in pitch are said to be in unison. This fact, though simple, has a most important physiological bearing. In the first place, an educated ear can, without difficulty, distinguish slight differences in pitch in ordinary musical tones. Again, we ascertain by experiment that this power of appreciation of tones is restricted within well-defined limits, which vary slightly in different individuals. Without citing all of the numerous observations upon this point, we may state that Helmholtz, whose authority is the very highest, gives, as the range of sounds that can be legitimately employed in music, those of from 40 to 4,000 vibrations in a second, embracing about seven octaves. In an orchestra, the double bass gives the lowest note, which has 40·25 vibrations in a second, and the highest note, given by the small flute, has 4,752 vibrations. In grand organs, there is a pipe which gives a note of 16·5 vibrations, and the deepest note of modern pianos has 27·5 vibrations; but delicate shades of pitch in these low notes are not appreciable to most persons. Sounds above the limits just indicated are painfully sharp, and their pitch cannot be exactly appreciated by the ear. The physiological interest connected with these facts is, that the limits of the appreciation of musical sounds are probably due to the anatomical arrangement of the auditory apparatus, as we have a limit to the acuteness of vision, which can be explained by the structure of the eye. This fact is the basis of the accepted theories of the appreciation of musical sounds.

Musical Scale.—We have thus far considered musical sounds, without any reference to the relations of different notes to each other. A knowledge of these relations lies at the foundation of the science of music; and, without a clear idea of certain of the fundamental laws of music, we cannot thoroughly comprehend the mechanism of audition.

It requires very little cultivation of the ear to enable us to comprehend the fact, that the successions and combinations of tones must obey certain fixed laws; and, long before these laws were the subject of mathematical demonstration, the relations of the different notes of the scale were established, merely because certain successions and combinations were agreeable to the ear, while others were discordant and apparently unnatural. Now that we are pretty thoroughly acquainted with the laws of vibrations, we can study the scale from a scientific, as well as from an æsthetic point of view.

The most convenient notes for our study are those produced by vibrating strings, and the phenomena here observed are essentially the same for all musical sounds; for it is by means of vibrations communicated to the air that the waves of sound find their way to the auditory apparatus. Let us take, to begin with, a string vibrating 24 times in a second. If this string be divided into two equal parts, each part will vibrate 48 times in a second. The note thus produced is the octave, or the 8th of the primary note, called the 8th, because the natural scale, as we shall see, contains eight notes, of which the first is the lowest and the last, the highest. We may divide the half again, producing a second octave, and so on, within the limits of our appreciation of musical sounds. If we divide the string so that $\frac{2}{3}$ of its length will vibrate, we have 36 vibrations in a second, and this note is the 5th in the scale. If we divide the string again, so as to leave $\frac{4}{5}$ of its length, we have 30 vibrations, which gives the 3d note in the scale. These are the most natural subdivisions of the note; and the 1st, 3d, 5th, and 8th, when sounded together, make what is known as the common major chord. Three-fourths of the length of the original string makes 32 vibrations, and gives the 4th note in the scale. If we take $\frac{8}{9}$ of the string, we have 27 vibrations, and the note is the 2d in the scale. With $\frac{3}{5}$ of the string, we have 40 vibrations in a second, or the 6th note in the scale. With $\frac{8}{15}$ of the string, we have 45 vibrations in a second, or the 7th note in the scale.

It will be observed that we have started with a note, which we may call C. This is the key-note, or the tonic. In this scale, which is called the natural, or diatonic key, we have a regular mathematical progression from the 1st to the 8th. This is called the major key of C. Melody consists in an agreeable succession of notes, which we may assume, for sake of simplicity, to be pure. We cannot, in a simple melody, sound any note but one of those in the scale. When a different note is sounded, we pass into a key which has a different fundamental note, or tonic, with a different succession of 3ds, 5ths, etc. Every key, therefore, has its 1st, 3d, 5th, and 8th, as well as the intermediate notes. If we substitute for the 3d a note formed by a string $\frac{5}{6}$ the length of the tonic instead of $\frac{4}{5}$, we have the key converted into the minor. The minor chord, consisting of the 1st, the diminished 3d, the 5th, and the 8th, is perfectly harmonious, but it has a quality quite different from that of the major chord. The notes of a melody may progress in the minor key as well as in the major. Taking the small numbers of vibrations merely for convenience, the following is the mode of progression in the natural scale of C major:

	1st.	2d.	3d.	4th.	5th	6th.	7th.	8th.
Note	C	D	E	F	G	A	B	C
Lengths of the string	1	$\frac{8}{9}$	$\frac{4}{5}$	$\frac{3}{4}$	$\frac{2}{3}$	$\frac{3}{5}$	$\frac{8}{15}$	$\frac{1}{2}$
Number of vibrations	24	27	30	32	36	40	45	48

The intervals between the notes of the scale, it is seen, are not equal. The smallest, between the 3d and 4th and the 7th and 8th, are called semitones. The other intervals are either full perfect tones or small perfect tones. Although there are semitones, not belonging to the key of C, between C and D, D and E, F and G, G and A, and A and B, these intervals are not all composed of exactly the same number of vibrations; so that, taking the notes on a piano, if we have D as the tonic, its 5th would be A. We assume that D has 27 vibrations, and A, 40, giving a difference of 13. With C as the tonic and G as the 5th, we have a difference of 12. It is on account of these differences in the intervals, that each key in music has a peculiar and an individual character.

In tuning a piano, which is the single instrument most commonly used for accompaniment and the general interpretation of musical compositions, the ordinary method is by the 5ths. We bring the 5th of C in exact accord with the tonic; then the 5th of D; then the 5th of E, and finally the 5th of F. The 5th of F should be the octave of C, but, by progressing in this way, the last note (C) is too sharp and is not the octave of the lower C. If this progression were continued higher and higher, the octaves would become more and more out of tune; and, to avoid this, the octaves are made perfect and the 5ths and 3ds are tuned down, so that the inequality is distributed throughout the scale. This is called tempering the scale, and, with this "temperament," the notes are not exactly true; still, musicians are accustomed to this, and they fail to recognize the mathematical defect.

Even in melody, and still more in harmony, in long compositions, the ear becomes fatigued by a single key, and it is necessary, in order to produce the most pleasing effects, to change the tonic, by what is called modulation, returning afterward to the original key.

Quality of Musical Sounds.—By appropriate means, we can analyze or decompose white light into prismatic colors; and, in the same way, nearly all musical sounds, which seem at first to be simple, can be resolved into certain well-defined constituents. There are few absolutely simple sounds used in music. We may take an example, however, in the notes of great stopped-pipes in the organ. These are simple, but are of an unsatisfactory quality and wanting in richness. Almost all other musical sounds, however, have a fundamental tone, which we recognize at once; but this tone is accompanied by harmonics caused by secondary vibrations of subdivisions of the sonorous body. The number, pitch, and intensity of these harmonic, or aliquot vibrations affect what is called the quality, or timbre of musical notes, by modifying the form of the sonorous waves. This fact, which we shall discuss more elaborately farther on, requires little argument for its support. If we suppose a string vibrating a certain number of times in a second, the vibrations being perfectly simple, we should have, according to the laws of vibrating bodies, a simple musical tone; but, if we suppose that the string subdivides itself into different segments, one of which gives the 3d, another, the 5th, and so on, of the fundamental tone, it is evident that the form of the vibrations must be considerably modified. This is the fact; and, with these modifications in form, the quality, or timbre of the note is changed. We can illustrate this roughly on the piano. If we strike the note C, we have a certain quality of sound. We may assume, for sake of argument, that this is a simple tone, although in reality it is complex. We now strike simultaneously the fundamental note, its 3d, 5th, and 8th, making the common chord of C major. The predominant note is still C, but the addition of the harmonious notes modifies its quality.

If we diminish the third by a semitone, we still have C for the predominant note, but the quality of the chord is changed to the minor. In this rough illustration, the ear can readily detect the harmonious tones; but, in the note of a single string, this cannot be done without practice and close attention. Still, in the notes of single strings, the ear can distinguish the harmonics; and, what is more satisfactory, the existence of harmonics can be actually demonstrated in various ways.

From what we have just stated, it follows that nearly all musical tones consist, not only of a fundamental sound, but of harmonic vibrations, subordinate to the fundamental and qualifying it in a particular way. These harmonics may be feeble or intense; certain of them may predominate over others; some, that are usually present, may be eliminated; and, in short, there may be a great diversity in their arrangement, and thus the timbre may present an infinite variety. This is one of the elements entering into the composition of notes, and it affords a partial explanation of quality.

Another element in the quality of notes depends upon their reënforcement by resonance. The vibrations of a stretched string, not connected with a resonant body, are almost inaudible. In musical instruments, we have the sound taken up by some mechanical arrangement, as the sound-board of the organ, piano, violin, harp, guitar, etc. In the violin, for example, the sweetness of the tone depends chiefly upon the construction of the resonant part of the instrument, and but little upon the strings themselves, which are frequently changed. The same is true of the human voice, of wind-instruments, etc.; but we could not discuss these points elaborately, without giving a full description of the various musical instruments in common use, which would be out of place in a work upon physiology.

In addition to the harmonic tones of sonorous bodies, various discordant sounds are generally present, which modify the timbre, producing, usually, a certain roughness, such as the grating of a violin-bow, the friction of the columns of air against the angles in wind-instruments, etc. All of these conditions have their effect upon the quality of tones; and these discordant sounds may exist in infinite number and variety. These sounds are composed of irregular vibrations and are consequently inharmonious. Nearly all notes that we speak of in general terms as musical are composed of musical, or harmonic aliquot tones with the discordant elements to which we just alluded.

Aside from the relations of the various component parts of musical notes, the quality depends largely upon the form of the vibrations. To quote the words of Helmholtz, "the more uniformly rounded the form of the wave, the softer and milder is the quality of the sound. The more jerking and angular the wave-form, the more piercing the quality. Tuning-forks, with their rounded forms of wave, have an extraordinarily soft quality; and the qualities of sound generated by the zither and violin resemble in harshness the angularity of their wave-forms."

Harmonics, or Overtones.—As we have stated in the foregoing discussion, nearly all sounds are composite, but some contain many more aliquot, or secondary vibrations than others. The notes of vibrating strings are peculiarly rich in harmonics, and these may be used for illustration, remembering that the phenomena here observed have their analogies in nearly all varieties of musical sounds. If a stretched string be made to vibrate, the secondary tones, which qualify, as it were, the fundamental, are called harmonics, or, in German, overtones, a term which is now much used by English writers.

While it is difficult at all times to distinguish by the ear the individual overtones of vibrating strings, their existence can be demonstrated by a few simple experiments. Let us suppose, for example, that we have a string, the fundamental tone of which is C. We damp this string with a feather at one-fourth of its length and draw a violin-bow across the smaller section. We then sound, not only the fourth part of the string across which the bow is drawn, but the remaining three-fourths; but, if we have placed little riders of paper upon the longer segment, at distances equal to one-fourth the entire string, they will remain undisturbed, while riders placed at any other portion of the string will be thrown off. This experiment shows that the three-fourths of the string have been divided, as we have sounded the second octave above the fundamental tone. This may be illustrated by connecting one end of the string with a tuning-fork. When this is done, and the string is brought to the proper degree of tension, it will first vibrate as a whole, then, when a little tighter, will spontaneously divide into two equal parts, and, under increased tension, into three, four, and so on. By damping a string with the light touch of a feather, we suppress the fundamental tone and bring out the overtones, which exist in all vibrating strings, but are usually concealed by the fundamental. The points which mark the subdivisions of the string into segments of secondary vibrations are called nodes. When we damp the string at its centre, we quench the fundamental tone and have overtones an octave above; damping it at a distance of one-fourth, we have the second octave above, and so on. When we damp it at a distance of one-fifth from the end, we have the four-fifths sounding the 3d of the fundamental, with the second octave of the 3d. If we damp it at a distance of two-thirds, we have the 5th of the fundamental, with the octave of the 5th.

Every vibrating string possesses, thus, a fundamental tone and overtones. We have, qualifying the fundamental, first, as the most simple, a series of octaves; next, a series of 5ths of the fundamental and their octaves; and next, a series of 3ds. These are the most powerful overtones, and they form the common chord of the fundamental; but they are so far concealed by the greater intensity of the fundamental, that they cannot be easily distinguished by the unaided ear, unless the fundamental be quenched in some such way as we have indicated. In the same way, the harmonic 5ths and 3ds overpower other overtones; for we have the string subdividing again and again into overtones, which are not harmonious like the notes of the common chord of the fundamental.

The presence of overtones, resultant tones, and additional tones, which latter will be described hereafter, can be demonstrated, without damping the strings, by the resonators, invented by Helmholtz. It is well known that, if a glass tube, closed at one end, which contains a column of air of a certain length, be brought near a resounding body emitting a note identical with that produced by the vibrations of the column of air, the air in the tube will resound in consonance with the note. If, for example, we have a tube sounding C, a tuning-fork of the same pitch sounded near the tube will throw the air in the tube into action and will produce a powerful sound, while no other note will have this effect. The resonators of Helmholtz are constructed upon this principle. A glass globe or tube (Fig. 262) is constructed so as to produce a certain note. This has a larger opening (a) and a smaller opening (b) which latter is fitted in the ear by warm sealing-wax, the other ear being closed. When the proper note is sounded, it is reënforced by the resonator and is greatly increased in intensity, while all other notes are heard very faintly. Suppose, now, that we apply this to the detection of overtones. We fix in the ear a resonator adjusted to G, and sound the fundamental (C). The fundamental (C) is imperfectly heard, but the overtone (G) is reënforced, and we have a loud and distinct sound of the 5th. By using resonators graduated to the musical scale, we can easily analyze a note and distinguish the overtones. In the same way, if we place in the ear a resonator tuned to a particular note and strike a succession of chords on the piano, the general sound is imperfectly heard; but, whenever we strike the note of the resonator, this is clearly distinguished, to the practical exclusion of all others; and we can thus analyze complicated chords into each of their constituent parts. This experiment shows the similarity between chords, resolved into their constituent parts, and single notes, resolved into their harmonics, or overtones. The resonators of Helmholtz, which are open at the larger extremity, are infinitely more delicate than those in which this is closed by a membrane.

A very striking and instructive point in the present discussion is the following: All the overtones are produced by vibrations of segments of the string included between the comparatively still points, called nodes; and, if we cause a string to vibrate by plucking or striking it at one of these nodal points, we abolish the overtones which vibrate from this node at a fixed point. For example, if we pluck the string at its exact centre, we sound the fundamental; but we then have a dull tone, which is deficient in the overtones of the octaves. We can demonstrate the fact that these overtones are absent, for, if we damp the string at its centre, the fundamental is quenched, but we have no octaves, which are always heard on damping the centre when the string is plucked at other points. In the same way, by plucking the string at different points, we can abolish the overtones of

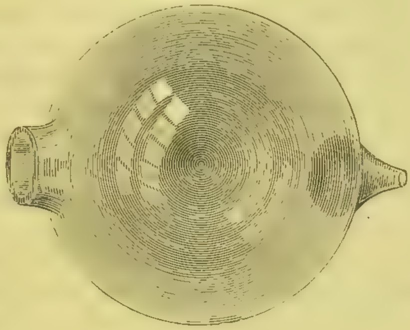


FIG. 262 *a*.

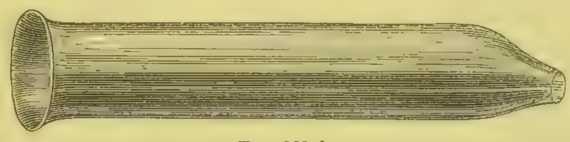


FIG. 262 *b*.

FIG. 262.—*Resonators of Helmholtz.*

5ths, 3ds, etc. It is readily understood that, when a string is plucked at any point, it will vibrate so vigorously at this point that no node can be formed. This fact has long been recognized by practical musicians, although many are probably unacquainted with its scientific explanation. Performers upon stringed instruments habitually attack the strings near their extremities. In the piano, where the strings may be struck at almost any point, the hammers are placed at from $\frac{1}{9}$ to $\frac{1}{7}$ of their extremities; and it has been ascertained by experience that this gives the richest notes. The nodes formed at these points would produce the 7ths and 9ths as overtones, which do not belong to the perfect major chord, while the nodes for the harmonious overtones are undisturbed. The reason, then, why the notes are richer and more perfect when the strings are attacked at this point, is that the harmonious overtones are full and perfect, and certain of the discordant overtones are suppressed.

When two harmonious notes are produced under favorable conditions, we can hear, in addition to the two sounds, a sound differing from both and much lower than the lower of the two. This sound is too low for an harmonic, and it has been called a resultant tone. The formation of a new sound by combining two sounds of different pitch is analogous to the blending of colors in optics, except that the primary sounds are not lost. The laws of the production of these resultant sounds are very simple. When two notes in harmony are sounded, the resultant tone is equal to the difference between the two primaries. For example, if we sound C, with 48 vibrations, and its 5th, with 72 vibrations in a second, the resultant tone is equal to the difference, which is 24 vibrations, and it is consequently the octave below C; or, if we sound C, with 48 vibrations, and its 3d, with 60, we have a resultant tone two octaves below C, the number of vibrations being 12.[1] These resultant tones are very feeble as compared with the primary tones, and

[1] These numbers are used merely in illustration. A sound of 12 vibrations does not come within the musical scale.

they can be heard only under the most favorable experimental conditions. In addition to these sounds, Helmholtz has discovered sounds, even more feeble, which he calls additional, or summation tones. The value of these is equal to the sum of vibrations of the primary tones. For example, C (24) and its 5th (36) would give a summation tone of 60 vibrations, or the octave of the 3d; and C (24) with its 3d (30) would give 54 vibrations, the octave of the 2d. These tones can readily be distinguished by means of the resonators already described.

It is thus seen that musical sounds are excessively complex. With single sounds, we have an infinite variety and number of harmonics, or overtones, and in chords, which will be treated of more fully under the head of harmony, we have a series of resultants, which are lower than the primary tones, and a series of additional, or summation tones, which are higher; but both the resultant and the summation tones bear an exact mathematical relation to the primary tones of the chord.

Harmony.—We have discussed the overtones, resultant tones, and summation tones of strings rather fully, for the reason that, in the physiology of audition, we shall see that the ear is capable of recognizing single sounds or successions of single sounds; but, at the same time, certain combinations of sounds are appreciated and are even more agreeable than those which are apparently produced by simple vibrations. Combinations of tones which thus produce an agreeable impression are called harmonious. They seem to become blended with each other into a complete sound of peculiar quality, all of the different vibrations entering into their composition being simultaneously appreciated by the ear. From what we have learned of overtones, it is evident that few musical sounds are really simple, and that those which are simple are wanting in richness, while they are perfectly pure. The blending of tones which bear to each other a certain mathematical relation is called harmony; but two or more tones, though each one be musical, are not necessarily harmonious. The most prominent overtone, except the octave, is the 5th, with its octaves, and this is called the dominant. The next is the 3d, with its octaves. The other overtones are comparatively feeble. Reasoning, now, from our knowledge of the relations of overtones, we might infer that the reënforcement of the 5th and 3d by other notes bearing similar relations to the tonic would be agreeable. This is the fact, and it was ascertained empirically long before the pleasing impression produced by such combinations was explained mathematically. We do not propose to enter into a full discussion of the laws of harmony, but a knowledge of certain of these laws is essential to the comprehension of the physiology of audition. These are very simple, now that we have analyzed the sound of a single vibrating body.

It is a law in music, that the more simple the ratio between the number of vibrations in two sounds, the more perfect is the harmony. The simplest relation, of course, is 1 : 1, when the two sounds are said to be in unison. The next in order is 1 : 2. If we sound C and its 8th, we have, for example, 24 vibrations of one to 48 of the other. These sounds can produce no discord, because the waves never interfere with each other, and the two sounds can be prolonged indefinitely, always maintaining the same relations. The combined impression is therefore continuous. The next in order is the 1st and 5th, their relations being 2 : 3. In other words, with the 1st and 5th, for two waves of the 1st we have three waves of the 5th. The two sounds may thus progress indefinitely, for the waves coincide for every second wave of the 1st and every third wave of the 5th. The next in order, if we sound at the same time the 1st, 5th, and 8th, is the 3d. The 3d of C has the 8th of C for its 5th, and the 5th of C for its minor 3d. The 1st, 3d, 5th, and 8th form the common major chord; and the waves of each tone blend with each other at such short intervals of time that the ear experiences a continuous impression, and no discord is appreciated. This explanation of the common major chord illustrates the law that, the smaller the ratio of vibration between different tones, the more perfect is their harmony. Sounded with the 1st, the 4th is more harmonious than the 3d; but its want of harmony with the 5th excludes it from the common chord. The 1st, 4th, and 8th are harmonious, but to make a complete chord we must use the 6th. These discussions might be extended into the progression of chords and modulation; but this is not essential to our purpose, as we wish only to ascertain the laws of the vibrations of sounds in harmony and the mechanism of discords.

Discords.—A knowledge of the mechanism of simple accords enables us to understand more easily the rationale of discords, and *vice versa.* As in the case of harmony, the fact that certain combinations of musical tones produce a disagreeable impression was ascertained empirically, with no knowledge of the exact cause of the palpable dissonance. Thanks to the labors of modern physicists, however, the mechanism of discords is now pretty well settled. We shall, in our explanation, begin with a combination of tones slightly removed from perfect unison.

Suppose, for example, that we have two tuning-forks giving precisely the same numbers of vibrations in a second; the tones are then in perfect unison. We load one of the forks with a bit of wax, so that its vibrations are slightly reduced, and start them both in vibration at the same instant. Taking the illustration given by Tyndall, we assume that one fork has 256, and the other, 255 vibrations in a second. While these two forks are vibrating, we have one gradually gaining upon the other; but, at the end of half a second, one will have made 128 vibrations, while the other will have made 127½. At this point the two waves are in direct opposition to each other; they are moving in exactly opposite directions; and, as a consequence, the sounds neutralize each other, and we have an instant of silence. The perfect sounds, as the two forks continue to vibrate, are thus alternately reënforced and diminished, and we have what are known in music as beats. As the difference in the number of vibrations in a second is one, we have the instants of silence occurring once in a second; and in this illustration the beats occur once a second. Unison takes place when two sounds can follow each other indefinitely, their waves blending perfectly; dissonance is marked by successive beats, or pulses. If we now load forks so that one will vibrate 240 times in a second, and the other 234, there will be six times in a second when the interference will be manifest; or, to make it plainer, in $\frac{1}{6}$ of a second, one fork will make 40 vibrations, while the other is making 39. We shall then have 6 beats in a second. From these experiments, the law may be deduced, that the number of beats produced by two tones not in harmony is equal to the difference between the two rates of vibration. An analogous interference of undulations is observed in optics, when waves of light are made to interfere and produce darkness.

It is evident that the number of beats will increase as we sound two discordant tones higher and higher in the scale. According to Helmholtz, the beats can be recognized up to 132 in a second. Beyond that point they become confused, and we have only a sensation of dissonance, or roughness. We can illustrate this point very satisfactorily by a simple experiment upon the piano. Let us take two tones, the highest on the scale, separated from each other by a semitone. When we strike these two notes together, we have a disagreeable sensation of dissonance, but no appreciable beats, because, the rate of vibration of each note being high, the difference is great and the beats are too rapid to be appreciated as such. We strike, now, the two notes an octave below; still we have dissonance, less disagreeable, but no beats. Passing down, an octave at a time, as the numbers of vibrations become smaller, the difference between them is less, and there are fewer beats in a second, until they are readily appreciated as beats and can even be counted. Beats, then, are due to interference of sound-waves, and the number in a second is equal to the difference in the rate of vibrations. When these are too rapid to be appreciated as beats, we have simply a sensation of discord. There is no interference of the waves of tones in unison, provided the waves start at the same instant; the intensity of the sound being increased by reënforcement. The differences between the 1st and 8th, the 1st and 5th, the 1st and 3d, and other harmonious combinations, is so great that we have no beats and no discord, the more rapid waves reënforcing the harmonics of the primary sound. It is important to remember, in this connection, that resultant tones are equal to the difference in the rates of vibration of two harmonious tones. If we take a note of 240 vibrations, and its 5th, with 360 vibrations, these two have a difference of 120, which is the lower octave of the 1st and is a harmonious tone.

It is evident that the laws which we have thus stated are equally applicable to overtones, resultant tones, and additional tones, which have their beats and dissonances, as well as the primary tones.

Tones by Influence (*Consonance*).—The term consonance is generally applied to the harmonious combinations of two or more sounds, and is synonymous with accord, as it is used in music. In this sense, it is opposed to dissonance, or discord. By some writers, however, consonance is used to denote sounds produced in sonorous bodies by the influence of sounds in unison. If, for example, we have a bell tuned to a certain note and bring near its opening a tuning-fork vibrating in unison with this note, the bell will sound vigorously in unison, although it is influenced only by the vibrations in the air produced by the primary sound. We have already spoken of this under the head of resonance; and sounds produced in this way are properly called tones by influence. Some physicists designate these as sympathetic vibrations. Dr. Elsberg, of New York, uses the term co-vibration and co-sounding, as applied to these phenomena.

It is evident that the mechanism of the production of tones by influence cannot be neglected in studying the physiology of audition. We have, as an important part of the auditory apparatus, the membrane of the tympanum, capable of various degrees of tension, which is thrown into vibration in obedience to waves of sound conducted by the atmosphere; and it will be an important point to determine how far the vibrations of this membrane are affected by the laws of the production of tones by influence.

After what we have learned of the laws of musical vibrations, it will be easy to comprehend the production of sounds by influence. We shall take first the most simple example, applied to strings. If we gently touch the note C upon the piano, so as to raise the damper but not sound the string, and then sing a note in unison, the string will return the sound, by the influence of the sound-waves. The sound thus produced by the string will have its fundamental tone and overtones; but the series of overtones will be complete; for none of the nodes are abolished, as in striking or plucking the string at any particular point. If, instead of the note in unison, we sing any of the octaves, the string will return the note sung; and the same is true of the 3d, 5th, etc. If we now strike a chord in harmony with the undamped string, this chord will be exactly returned by influence. In other words, a string may be made to sound by influence, its fundamental tone, its harmonics, and harmonious combinations. To carry the observation still farther, the string will return, not only a note of its exact pitch and its harmonics, but notes of the quality of the primary note. This is a very important point in its applications to the physiology of hearing and can be readily illustrated. Taking identical notes in succession, produced by the voice, trumpet, violin, clarinet, or other musical instruments, it can be easily noted that the quality of the note, as well as the pitch, is rendered by a resounding string; and the same is true of combinations of notes.

The above laws of tones by influence have been illustrated by strings merely for the sake of simplicity; but they have a more or less perfect application to all bodies capable of producing musical tones, except that some are thrown into vibration with more difficulty than others. An interesting application of these laws, however, particularly with reference to the physiology of the ear, is in the case of stretched membranes; for this brings to our mind the possible action of the membrana tympani.

If we have a thin membrane, like a piece of bladder or thin rubber, stretched over a circular orifice, such as the mouth of a wide bottle, this can be tuned to a certain note.

When arranged in this way, the membrane can be made to sound its fundamental note by influence. In addition, the membrane, like a string, will divide itself so as to sound the harmonics of the fundamental, and it will likewise be thrown into vibration by the 5th, 3d, etc., of its fundamental tone, thus obeying the laws of vibrations of strings, though the harmonic sounds are produced with greater difficulty.

Uses of Different Parts of the Auditory Apparatus.

The uses of the pavilion of the ear and of the external auditory meatus are sufficiently apparent. The pavilion serves to collect the waves of sound, and probably it inclines them toward the external meatus as they come from various directions. Although this action is simple, it undoubtedly has a certain degree of importance, and the various curves of the concavity of the pavilion tend more or less to concentrate the sonorous vibrations. Such has long been the opinion of physiologists, and this seems to be carried out by experiments in which the concavities of the external ear have been obliterated by wax. There is, probably, no resonance or vibration of much importance until the waves of sound strike the membrana tympani. The same remarks may be made with regard to the external auditory meatus. We do not know precisely how the obliquity and the curves of this canal affect the waves of sound, but we may suppose that the deviation from a straight course protects, to a certain degree, the tympanic membrane from impressions that might otherwise be too violent.

Structure of the Membrana Tympani.—The general arrangement of the membrana tympani has already been described in connection with the topographical anatomy of the auditory apparatus. This structure, which is of great importance in the physiology of hearing, is delicate, elastic, about the thickness of ordinary gold-beater's skin, and is subject to various degrees of tension, from the action of the muscles of the middle ear and different conditions of atmospheric pressure within and without the cavity of the tympanum. Its form is nearly circular. From a number of accurate measurements of its diameter in the adult, by Sappey, we may assume that its ring measures a little more than $\frac{2}{5}$ of an inch vertically and about $\frac{2}{5}$ of an inch antero-posteriorly. The excess of the vertical over the horizontal diameter is about $\frac{1}{25}$ of an inch. Notwithstanding the assertion of some of the older anatomists, that the tympanic membrane presents one or two small perforations, it is now almost universally regarded as forming a complete division, without openings, between the external meatus and the middle ear; or, if any openings exist, they are exceedingly minute.

The periphery of the tympanic membrane is received into a little ring of bone, which may be separated by maceration in early life, but which is consolidated with the adjacent bony structures in the adult. This bony ring is incomplete at its superior portion, but, aside from this, it resembles the groove which receives the crystal of a watch. At the periphery of the membrane, is a ring of condensed fibrous tissue, which is received into the bony ring. This ring also presents a break at its superior portion.

The concavity of the membrana tympani presents outward, and it may be increased or diminished by the action of the muscles of the middle ear. The point of greatest concavity, where the extremity of the handle of the malleus is attached, is called the umbo. Upon the inner surface of the membrane are two pouches, or pockets. One is formed by a small, irregular, triangular fold, situated at the upper part of its posterior half and consisting of a process of the fibrous layer. This, which is called the posterior pocket, is open below and extends from the posterior upper border of the membrane to the handle of the malleus, which it assists in holding in position. "After it has been divided, the bone is much more movable than before." (Tröltsch.) The anterior pocket is lower and shorter than the posterior. It is formed by a small bony process turned toward the neck of the malleus, by the mucous membrane, by the bony process of the malleus, by its anterior ligament, the chorda tympani, and the anterior tympanic artery. The handle of the malleus is inserted between the two layers of the fibrous structure of the membrana tympani and occupies the upper half of its vertical diameter, extending from the periphery to the umbo.

The membrana tympani, though thin and translucent, presents three distinct layers. Its outer layer is an excessively delicate prolongation of the integument lining the external meatus, presenting, however, neither papillæ nor glands. The inner layer is a delicate continuation of the mucous membrane lining the tympanic cavity and is covered by

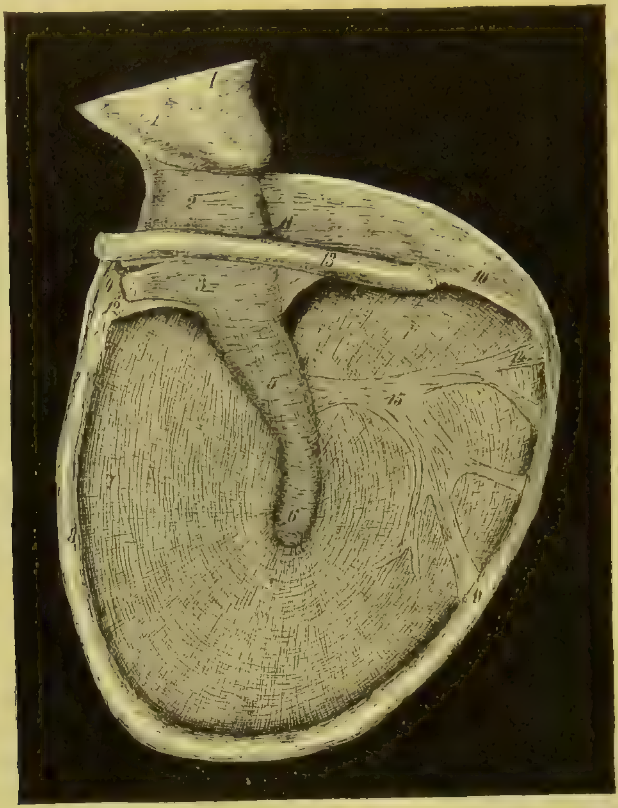


FIG. 263.—*Right membrana tympani, seen from within.* From a photograph, and somewhat reduced. (Rüdinger.)

1, head of the malleus, divided; 2, neck of the malleus; 3, handle of the malleus, with the tendon of the tensor tympani muscle; 4, divided tendon of the tensor tympani; 5, 6, portion of the malleus between the layers of the membrana tympani; 7, outer (radiating) and inner (circular) fibres of the membrana tympani; 8, fibrous ring of the membrana tympani; 9, 14, 15, dentated fibres, discovered by Gruber; 10, posterior pocket; 11, connection of the posterior pocket with the malleus; 12, anterior pocket; 13, chorda tympani nerve.

tessellated epithelial cells. The fibrous portion, or lamina propria, is formed of two layers. The outer layer consists of fibres, radiating from the handle of the malleus to the periphery. These are best seen near the centre. The inner layer is composed of circular fibres, which are most abundant near the periphery and diminish in number toward the centre.

The color of the membrana tympani, when it is examined with an aural speculum by daylight, is peculiar, and it is rather difficult to describe, as it varies in the normal ear in different individuals. Politzer describes the membrane, examined in this way, as translucent, and of a color which "most nearly approaches a neutral gray, mingled with a weaker tint of violet and light yellowish-brown. This color is modified, in certain portions of the membrane, by the chorda tympani and the bones of the ear, which produce some opacity. The entire membrane in health has a soft lustre. In addition, there is seen, with proper illumination, a well-marked, triangular cone of light, with its apex at the end of the handle of the malleus, spreading out in a downward and forward direction, and from $\frac{1}{16}$ to $\frac{1}{12}$ of an inch broad at its base. This appearance is regarded by pathologists as very important, as indicating a normal condition of the membrane. It is undoubtedly due to reflection of light, depending upon three factors, indicated by Roosa as follows: "First, the inclination of the membrana tympani to the auditory canal; second, the traction of the malleus, which renders it concave at the centre; third, its polish or brilliancy." With this explanation, it is not admitted that the light spot is due to a peculiar structure of that portion of the membrane upon which it is seen.

Uses of the Membrana Tympani.—It is unquestionable that the membrana tympani is very important in audition. In cases of disease in which the membrane is thickened, perforated, or destroyed, the acuteness of hearing is always more or less affected. That this is in great part due to the absence of a vibrating surface for the reception of waves of sound, is shown by the relief which is experienced by those patients who can tolerate the presence of an artificial membrane of rubber, when this is introduced. As regards the mere acuteness of hearing, aside from the pitch of sounds, the explanation of the action of the membrane is very simple. Sonorous vibrations are not readily transmitted through the atmosphere to solid bodies, like the bones of the ear; and when they are thus transmitted they lose considerably in intensity. When, however, the aërial vibrations are received by a delicate membrane, under the conditions of the membrana tympani, they are transmitted with very little loss of intensity; and, if this membrane be connected with solid bodies, like the bones of the middle ear, the vibrations are readily conveyed to the sensory portions of the auditory apparatus. The parts composing the middle ear are thus admirably adapted to the transmission of sonorous waves to the auditory nerves. The membrane of the tympanum is delicate in structure, stretched to the proper degree of tension, and vibrates under the influence of the waves of sound. Attached to this membrane, is the chain of bones, which conducts its vibrations, like the bridge of a violin, to the liquid of the labyrinth. The membrane is fixed at its periphery and has air upon both sides, so that it is under the most favorable conditions for vibration.

A study of the mechanism of the ossicles and muscles of the middle ear shows that the membrana tympani is subject to certain physiological variations in tension, due to contraction of the tensor tympani. It is also evident that this membrane may be drawn in and rendered tense by exhausting or rarefying the air in the drum. If the mouth and nose be closed and we attempt to breathe forcibly by expanding the chest, the external pressure tightens the membrane. In this condition, the ear is rendered insensible to grave sounds, but high-pitched sounds appear to be more intense. If the tension be relieved, as may be done by an act of swallowing, the grave sounds are heard with normal distinctness. This experiment, tried at a concert, produces the curious effect of abolishing a great number of the lowest tones, while the shrill sounds are heard very acutely. The same phenomena are observed when the external pressure is increased by descent in a diving-bell.

Undoubted cases of voluntary contraction of the tensor tympani have been observed by otologists; and in these, by bringing this muscle into action, the limit of the perception of high tones is greatly increased. In two instances of this kind, recorded by Dr. Blake, of Boston, the ordinary limit of perception was found to be three thousand single vibrations; and, by contraction of the muscle, this was increased to five thousand single vibrations.

The membrana tympani undoubtedly vibrates by influence, when it is brought in accord with a given note. In other words, this membrane obeys the laws of consonance and vibrates strongly by the influence of sounds in unison or in harmony with its fundamental tone. The laws of vibrations by influence have already been fully discussed;

and it remains for us now to determine how far these laws are applicable to the physiology of the vibrations of the membrana tympani and the action of these vibrations in the accurate perception of musical sounds.

There are certain phenomena of vibration of the membrana tympani that must occur, as a physical necessity, under favorable conditions, which it is important to note in this connection; and these have hardly attracted sufficient attention at the hands of physiological writers. In the first place, this membrane must obey the laws of vibration by influence. It is undoubtedly thrown into vibration by irregular waves of noise, as contradistinguished from musical tones; but, when a tone is sounded in unison with its fundamental tone, or when the tone sounded is one of the octaves of its fundamental, it must undergo a vibration by influence, like an artificial membrane. If we suppose the membrane to be tuned in unison with a certain note, it will not only return this note by influence, but it will repeat its quality. Not only this, when a combination of harmonious tones is sounded, the combined sound will be returned, with all the shades in quality which the combined tones produce. On account of its small size, the sound produced by the exposed membrane itself cannot be heard; but that the membrane does vibrate by influence, has been proven by experiments with small particles of sand on its surface.

We are certainly justified in supposing that vibrations of the membrana tympani, too delicate to be revealed to the eye or the ear in objective experiments, may be appreciated by the auditory nerves as a subjective phenomenon. In other words, we can probably appreciate vibrations in our own tympanic membrane, when these would be too delicate to be observed by the eye or ear, in a membrane exposed and subjected to similar influences. This point must be accepted as probable; and it cannot be proven by direct experiment. If this be true, the most complex combinations of sound produced by an orchestra might be actually reproduced by the tympanic membrane, if this membrane were accurately tuned to the fundamental tone.

The arrangement of the muscles and bones of the middle ear admits of the possibility of tuning the membrana tympani with exquisite nicety. These muscles are sometimes so far under the control of the will that we can tighten the membrane to its limit by a voluntary effort; the muscles are of the striated variety, and are capable of rapid action; they are supplied with motor filaments from the cerebro-spinal system; the ear is fatigued by long attention to particular tones; persons not endowed with what is termed a musical ear cannot appreciate slight distinctions between different tones; the ear is capable of education in the appreciation of pitch and in following rapid successions of tones; and, in short, there are many points in the mechanism of the transmission of musical sounds in the ear that seem to involve muscular action. In the larynx, we are conscious of differences in the tension of the vocal chords only from differences in the character and pitch of the sounds produced; in the eye, we are conscious of the contraction of the muscle of accommodation from the fact that an effort enables us to see objects distinctly at different distances; and it is not impossible that, under ordinary conditions, the consciousness of contractions of the muscles of the middle ear may be revealed only by the fact of the correct appreciation of certain musical tones. Some persons can educate the ear so as to acquire what is called the faculty of absolute pitch; that is, without the aid of a tuning-fork or any musical instrument, they can give the exact musical value of any given tone. A possible explanation of this is that such persons may have educated the muscles of the ear so as to put the tympanic membrane in such a condition of tension as to respond to a given note and to recognize the position of this note in the musical scale. Finally, an accomplished musician, in conducting an orchestra, can, by a voluntary effort, direct his attention to certain instruments, and hear their notes distinctly, separating them, as it were, from the general mass of sound, can distinguish the faintest discords, and immediately designate a single instrument making a false note.

The fact that rapid successions of notes are readily appreciated does not of necessity argue against the possibility of following these notes with the muscles of the ear; for the muscles of the larynx may act so as to produce successions of notes as rapidly as they can be correctly appreciated. Nor does the fact that we must prepare the tympanic membrane for certain notes militate against the theory we have just given, for musical compositions present melodious successions in a certain scale, the notes of which bear well-defined harmonious relations to each other, and we immediately appreciate a change in the key, which is simply a change in the fundamental. These changes in the key must be made in accordance with the laws of modulation; otherwise they are harsh and grating. Modulation in music is simply a mode of passing from one key to another by certain transition-notes or chords, which seem inevitably to lead to a certain key, and to no other. Finally, the laws of vibration by influence show that a single vibrating membrane returns the quality as well as the pitch of tones and of combinations of tones as well.

The theory we have just given of the possible action of the membrana tympani is an elaboration of the view advanced by Everard Home. Unfortunately for the simplicity of the mechanism of hearing and the idea of division and isolation of function in different parts, which is so seductive to physiologists, there are certain facts and considerations which may prevent some from adopting it absolutely and exclusively as an explanation of the mechanism of the appreciation of musical sounds. These are the following:

Destruction of both membranæ tympani does not necessarily produce total deafness, although this condition involves considerable impairment of hearing. So long as there is simple destruction of these membranes, the bones of the middle ear and the other parts of the auditory apparatus being intact, the waves of sound are conducted to the auditory nerves, though imperfectly. In a remarkable case reported by Sir Astley Cooper, which is cited by most writers upon physiology, one membrana tympani was entirely destroyed, and the other was nearly gone, there being some parts of its periphery remaining. In this person, the hearing was somewhat impaired, although he could distinguish ordinary conversation pretty well. Fortunately, he had considerable musical taste, and it was ascertained that his musical ear was not seriously impaired; "for he played well on the flute and had frequently borne a part in a concert. I speak this, not from his authority only, but also from that of his father, who is an excellent judge of music, and plays well on the violin: he told me, that his son, besides playing on the flute, sung with much taste, and perfectly in tune." This single case, if its details be accurate—which we have no reason to doubt—shows conclusively that the correct appreciation of musical sounds may exist independently of the action of the membrana tympani.

There is one consideration, of the greatest importance, that must be kept in view in studying the functions of any distinct portion of the auditory apparatus, like the membrana tympani. This, like all other parts of the apparatus, except the auditory nerves themselves, has simply an accessory function. If the regular waves of a musical tone be conveyed to the terminal filaments of the auditory nerves, these waves make their impression and the tone is appreciated. It makes no difference, except as regards intensity, how these waves are conducted; the tone is appreciated by the impression made upon the nerves, and the nerves only. The waves of sound are not like the waves of light, refracted, decomposed, perhaps, and necessarily brought to a focus as they impinge upon the retina; as far as the action of the accessory parts of the ear are concerned, the waves of sound are unaltered; that is, the rate of their succession remains absolutely the same, though they be reflected by the concavities of the concha and repeated by the tympanic membrane. Even if we assume that the membrane, under normal conditions, repeats musical sounds by vibrations produced by influence, and that this membrane is tuned by voluntary muscular action so that tones are exactly repeated, the position of these tones in the musical scale is not and cannot be altered by the action of any of the accessory organs of hearing. The fact that a person may retain his musical ear with both membranes destroyed is not really an argument against the view that the membrane repeats tones by influence; for, if musical tones or noisy vibrations be conducted to the auditory nerves, the impression produced must of necessity be dependent exclusively upon the character, regularity, and number of the sonorous vibrations. And, again, the physical laws of sound, which are fixed and unchangeable, teach us that a membrane, like the membrana tympani, must return or reproduce sounds which are in unison or are harmonious with its fundamental tone, much more perfectly than discordant or irregular vibrations. In a loud confusion of noisy sounds, we can readily distinguish pure melody or harmony, even when the vibrations of the latter are comparatively feeble. In following with the ear any piece of music, reasoning from purely physical considerations, it must at times occur that the tones are in exact unison or in harmony with the fundamental tone of the membrana tympani. Supposing the fundamental tone of the membrane to be constant and invariable, such tones would be heard much more distinctly than others, as a physical necessity. Such a difference in the appreciation of certain notes in melody does not occur; and the only reasonable explanation of this is that the tension of the membrane is altered. It is shown by anatomical researches that the tension can be altered by muscular action, and, as the muscles are striated, we may suppose that it may be modified rapidly. Physiological observations show that such modifications in tension do occur; and there are on record unquestionable instances in which the membrana tympani is tightened by a voluntary contraction of the tensor tympani muscle.

Another important point to note in this connection is the following: Can it be shown that the appreciation of the pitch of tones bears any relation to the degree of tension of the tympanic membrane? We can answer this question unreservedly in the affirmative. When the membrane is rendered tense, there is insensibility to low tones. When the membrane is brought to the highest degree of tension by voluntary contraction of the tensor tympani, the limit of appreciation of high tones may be raised from three thousand to five thousand vibrations. It is a fact in the physics of the membrana tympani, that the vibrations are more intense the nearer the membrane approaches to a vertical position. It has also been shown that the membrane has a strikingly vertical position in musicians, and that the position is very oblique in persons with an imperfect musical ear. This fact has a most important bearing upon the probable relation between the membrana tympani and the correct appreciation of musical sounds.

In view of all facts and considerations for and against the theory which we have given of the action of the tympanic membrane in the appreciation of musical sounds, does it not seem probable that there are, acting upon this membrane, muscles of auditory accommodation, analogous in their operation to the muscle of visual accommodation? We have carefully studied this subject in all its bearings, and, if the reader follow closely our process of reasoning, it must seem probable that the muscles of the middle ear are muscles of auditory accommodation; but it should be remembered that the action of the membrane is not absolutely essential, and that musical tones, however conducted, must of necessity be correctly appreciated, whenever and however they find their way to the auditory nerves.

Experiments have shown pretty conclusively that the tympanic membrane vibrates more forcibly when relaxed than when it is tense. It is evident that the relaxed membrane must undergo vibrations of greater amplitude than when it is under strong tension. In certain cases of facial palsy, in which it is probable that the branch of the facial going to the tensor tympani was affected, the ear became painfully sensitive to powerful impressions of sound. This probably has no relation to pitch, and most sounds that are painfully loud are comparatively grave. The tension of the membrane may be modified as a means of protection of the ear, but the facts belonging to cases of facial palsy are all that we have bearing upon this point. Artillerists are in danger of rupture of the membrana tympani from sudden concussions. To guard against this injury, it is recommended to stop the ear, draw the shoulder up against the ear most in danger, and particularly to inflate the middle ear after Valsalva's method. "This method consists in making a powerful expiration, with the mouth and nostrils closed."

Mechanism of the Ossicles of the Ear.—The ossicles of the middle ear, in connection with the muscles, have a twofold function: First, by the action of the muscles, the membrana tympani may be brought to different degrees of tension. Second, the chain of bones serves to conduct sonorous vibrations to the labyrinth. It must be remembered that the handle of the malleus is closely attached to the membrana tympani, especially near its lower end. Near the short process, the attachment is looser and there is even an incomplete joint-space at this point. The long process is attached closely to the Glasserian fissure of the temporal bone.

The malleus is articulated with the incus by a very peculiar joint, which has been accurately described by Helmholtz. This joint is so arranged, presenting a sort of cog, that the handle of the malleus can rotate only outward; and, when a force is applied which would have a tendency to produce a rotation inward, the malleus must carry the incus with it. This mechanism has been aptly compared by Helmholtz to that of a watch-key with cogs which are fitted together and allow the whole key to turn in one direction, but are separated so that only the upper portion of the key turns when the force is applied in the opposite direction. In the articulation between the malleus and the incus, the only difference is that there is but one cog; but this is sufficient to prevent an independent rotation of the malleus inward. This enables us to understand the action of the tensor tympani muscle. By the contraction of this muscle, "all the bands which give firmness to the position of the ossicles are rendered tense. This muscle, in the first place, draws the handle of the hammer inward, and with it the membrana tympani. At the same time it pulls upon the axis-band of the hammer, drawing it inward and putting it upon the stretch. Another effect, as we have shown, is to draw the head of the hammer away from the tympano-incudal joint, to tighten all the ligaments of the anvil, those toward the hammer as well as those at the end of its short process, and to lift the latter up from its bony bed. In this way the anvil is brought into the position where the cogs of the malleo-incudal joint fit into one another the tightest. Finally, the long process of the anvil is compelled to form a rotation inward in company with the handle of the hammer; in so doing, as we shall see further on, it presses upon the stirrup and drives it into the oval window against the fluid of the labyrinth.

"In this respect the construction of the ear is very remarkable. By the contraction of the single mass of elastic fibres constituting the tensor tympani (whose tension, besides, is variable and may be adapted to the wants of the ear) all the inelastic tendinous ligaments of the ossicles are simultaneously put upon the stretch." (Helmholtz.)

The body of the incus is attached to the posterior bony wall of the tympanic cavity. Its articulation with the malleus has just been indicated. By the extremity of its long process, it is also articulated with the stapes, which completes the chain. *In situ*, the stapes forms nearly a right angle with the long process of the incus.

The stapes is articulated with the incus, as indicated above, and its oval base is applied to the fenestra ovalis. Surrounding the base of the stapes, is a ring of elastic fibro-cartilage, which is closely united to the bony wall of the labyrinth, by an extension of the periosteum over the base of the stapes.

"The relation of the stirrup to the anvil is such that, if the handle of the hammer be drawn inward, the long process of the anvil presses firmly against the knob of the stirrup; the same takes places if the capsular ligament between both be cut through." (Helmholtz.)

The articulations between the malleus and the incus and between the incus and the stapes are so arranged that, when the membrana tympani is forced outward, as it may be by inflation of the tympanic cavity, there is no danger of tearing the stapes from its attachment to the fenestra ovalis; for, when the handle of the malleus is drawn outward, the cog-joint between the malleus and the incus is loosened and no great traction can be exerted upon the stapes.

Although experiments have demonstrated pretty conclusively the mechanism of the ossicles and the action of the tensor tympani muscle, both as regards the chain of bones and the membrana tympani, direct observations are wanting to show the exact relations of these different conditions of the ossicles and of the membrane to the physiology of audition. One very important physical point, however, which has been the subject of much discussion, is settled. The chain of bones acts as a single solid body in conducting vibrations to the labyrinth. It is a matter of physical demonstration that vibrations of the bones themselves would be infinitely rapid as compared with the highest tones which can be appreciated by the ear, if it were possible to induce in these bones regular vibrations. Practically, then, the ossicles have no independent vibrations that we can appreciate. This being the fact, the ossicles simply conduct to the labyrinth the vibrations induced in the membrana tympani by sound-waves; and their arrangement is such that these vibrations lose very little in intensity. While it has been shown experimentally that the amplitude of vibration in the membrana tympani and the ossicles diminishes with the tension of the membrane, it would seem that, when the tensor tympani contracts, it must render the conduction of sound-waves to the labyrinth more delicate than when the auditory apparatus is in a relaxed condition, which we may compare with the "indolent" condition of the apparatus of accommodation of the eye. When the membrana tympani is relaxed and the cog-like articulation between the malleus and the incus is loosened, the vibrations of the membrane and of the malleus may have a greater amplitude; but, when the malleo-incudal joint is tightened and the stapes is pressed against the fenestra ovalis, the loss of intensity of vibration in conduction through the bones to the labyrinth must be reduced to the minimum. With this view, the tensor tympani muscle, while it contracts to secure for the membrana tympani the degree of tension most favorable for vibration under the influence of certain tones, puts the chain of bones in the condition best adapted to the conduction of the vibrations of the membrane to the labyrinth, with the smallest possible loss of intensity.

Physiological Anatomy of the Internal Ear.

The internal ear consists of the labyrinth, which is divided into the vestibule, semicircular canals, and cochlea. The general arrangement of these parts has already been described; and it remains for us only to study the structures contained within the bony labyrinth, in so far as their anatomy bears upon the physiology of audition. The most delicate and complicated points, by far, in the anatomy of the auditory apparatus are connected with the histology of the internal ear, which, since the researches of Corti, has been studied very closely, particularly in Germany. We shall avoid, however, the discussion of histological questions of purely anatomical interest and confine ourselves to those points which have a direct bearing upon physiology.

Passing inward from the tympanum, the first division of the internal ear is the vestibule. This cavity communicates with the tympanum by the fenestra ovalis, which is closed in the natural state by the base of the stapes. It communicates, also, with the semicircular canals and with the cochlea.

General Arrangement of the Membranous Labyrinth.—The bony labyrinth is lined by a moderately thick periosteum, consisting of connective tissue, a few delicate elastic fibres, numerous nuclei, and blood-vessels, with spots of calcareous concretions. This membrane adheres closely to the bone and extends over the fenestra ovalis and the fenestra rotunda. Its inner surface is smooth and covered with a single layer of cells of pavement-epithelium, which in some parts is segmented and in others forms a continuous nucleated sheet. In certain portions of the vestibule and semicircular canals, the periosteum is united to the membranous labyrinth, more or less closely, by fibrous bands, which have been called ligaments of the labyrinth. The fenestra rotunda, which lies between the cavity of the tympanum and the cochlea, is closed by a membrane formed by an extension of the periosteum lining the cochlea, on the one side, and the mucous membrane lining the tympanic cavity, on the other.

In the bony vestibule, occupying about two-thirds of its cavity, are two distinct sacs; a large, ovoid sac, the utricle, situated in the upper and posterior portion of the cavity, and a smaller, rounded sac, the saccule, situated in its lower and anterior portion. The

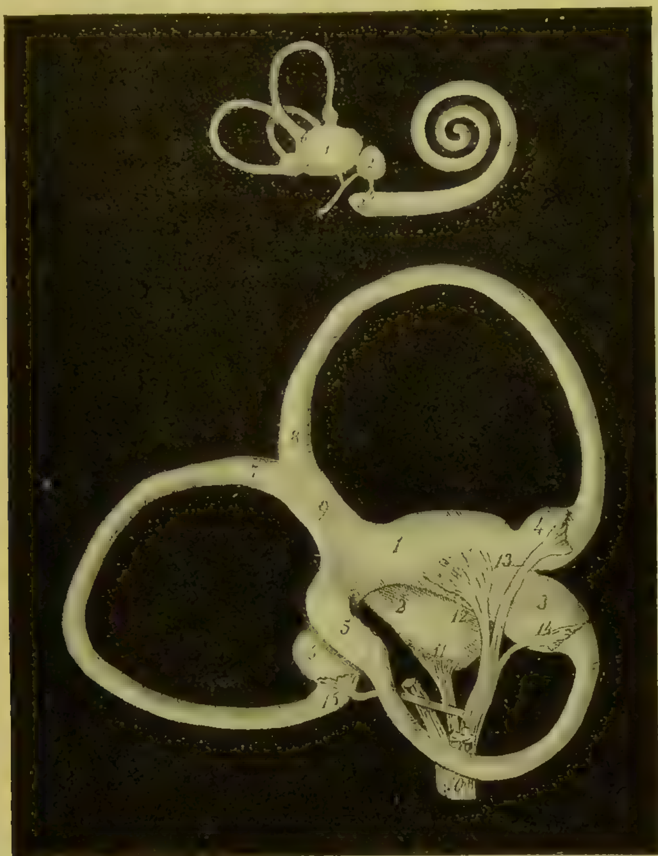


FIG. 264.—*Diagram of the labyrinth, vestibule, and semicircular canals.* From a photograph, and somewhat reduced. (Rüdinger.)

Upper figure: 1, utricle; 2, saccule; 3, 5, membranous cochlea; 4, canalis reuniens; 6, semicircular canals.
Lower figure: 1, utricle; 2, saccule; 3, 4, 6, ampullæ; 5, 7, 8, 9, semicircular canals; 10, auditory nerve (partly diagrammatic); 11, 12, 13, 14, 15, distribution of the branches of the nerve to the vestibule and the semicircular canals; 16, ganglioform enlargement.

utricle communicates with the semicircular canals; and the saccule opens into the membranous canal of the cochlea by the canalis reuniens. At a point in the utricle corresponding to the entrance of a branch of the auditory nerve, is a round, whitish spot, called the acoustic spot (macula acustica), containing otoliths, or otoconia, which are attached to the inner surface of the membrane. A similar spot, containing otoliths, exists in the saccule at the point of entrance of its nerve. Otoliths are also found in the ampullæ of the semicircular canals. These calcareous masses are composed of crystals of carbonate of lime, which are hexagonal and pointed at their extremities. Nothing definite is known of the function of these calcareous bodies, which exist in man, mammals, birds, and reptiles.

The membranous semicircular canals occupy about one-third of the cavity of the bony canals. They present little ovoid dilatations, called ampullæ, corresponding to the ampullary enlargements of the bony canals.

The membrane of the cochlea, including the lining periosteum, occupies the spiral canal of the cochlea, which it fills completely. Viewed externally, it appears as a single tube, following the turns of the bony cochlea, beginning below, at the first turn, by a blind extremity, and terminating in a blind extremity at the summit of the cochlea. If we make a section of the cochlea in a direction vertical to its coils, it will be seen that this canal is divided, partly by bone and partly by membrane, into an inferior portion, a superior portion, and a triangular canal, lying between the two, which is external. The bony septum is in the form of a spiral plate, extending from the central column (the modiolus) into the cavity of the cochlea, about half-way to its external wall, and terminating above in a hook-shaped extremity, called the hamulus. The free edge of this bony lamina is thin and dense. Near the central column, it divides into two plates, with an intermediate spongy structure in which are lodged vessels and nerves. The surface of the bony lamina looking toward the base of the cochlea is marked by numerous regular, transverse ridges, or striæ.

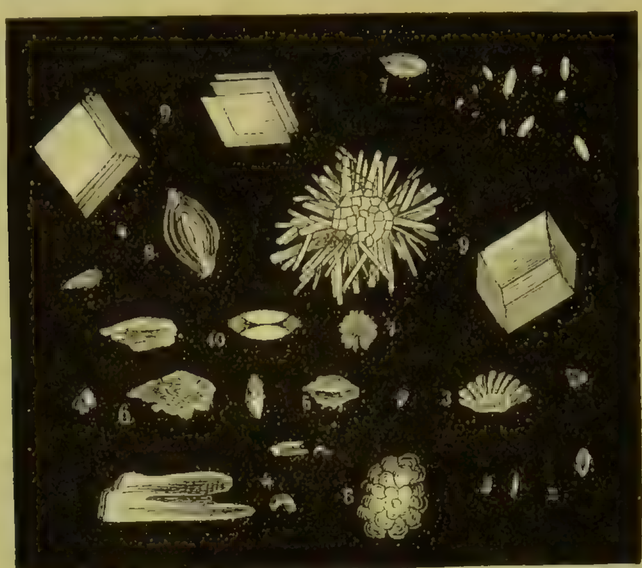


FIG. 265.—*Otoliths from various animals.* (Rüdinger.)
1, from the goat; 2, from the herring; 3, from the devil-fish; 4, from the mackerel; 5, from the flying-fish; 6, from the pike; 7, from the carp; 8, from the ray; 9, from the shark; 10, from the grouse.

Attached to the free margin of the bony lamina, is a membrane (the membrana basilaris) which extends to the outer wall of the cochlea. In this way, the canal of the cochlea is divided into two portions, one above and the other below the septum. The portion below begins at the fenestra rotunda and is called the scala tympani. The portion above, exclusive of the triangular canal of the cochlea, communicates with the vestibule and is called the scala vestibuli.

Above the membrana basilaris, is a membrane (the limbus laminæ spiralis) the external continuation of which is called the membrana tectoria, or the membrane of Corti. Between the membrana tectoria and the membrana basilaris, is the organ of Corti. The membrane of Reissner extends from the inner portion of the limbus upward and outward to the outer wall of the cochlea. This divides the portion of the cochlea situated above the scala tympani into two portions; an internal portion, the scala vestibuli, and an external, triangular canal, called the canalis cochleæ, or the membranous cochlea.

In the anatomical description of the contents of the bony cochlea, the membranous parts may be designated as follows:

1. The portion below the bony and membranous septum, called the scala tympani. This is formed by the periosteum lining the corresponding portion of the cochlea and the under surface of the bony lamina, and the membrana basilaris.

2. The scala vestibuli. This is formed by the periosteum lining the corresponding portion of the bony cochlea and the upper surface of the bony septum and is bounded externally by the membrane of Reissner.

3. The true membranous cochlea. This is the spiral triangular canal, bounded externally by the periosteum of the corresponding portion of the wall of the cochlea,

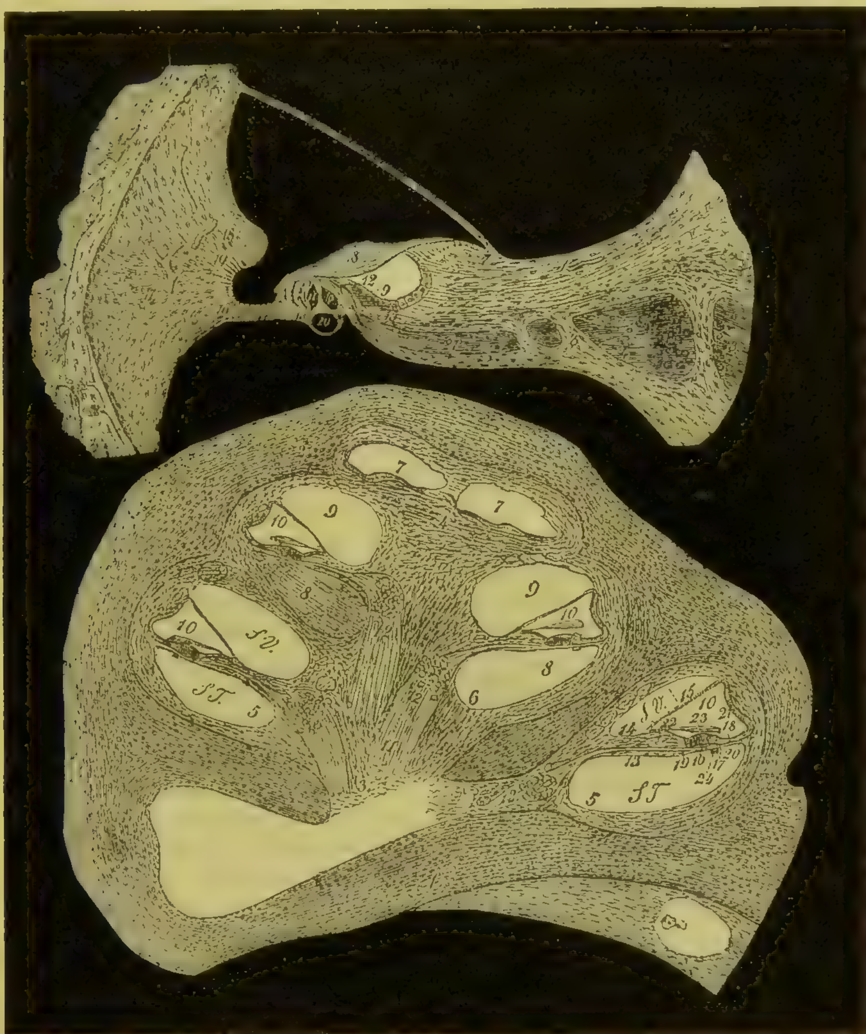


FIG. 266.—*Section of the first turn of the spiral canal of a cat newly-born.—Section of the cochlea of a human fœtus at the fourth month.* From a photograph, and somewhat reduced. (Rüdinger.)

Upper figure: 1, 2, 6, lamina spiralis; 2, lower plate; 3, 4, 5, 5, nervus cochlearis; 7, membrane of Reissner; 8, membrana tectoria; 9, epithelium; 10, 11, pillars of Corti; 12, inner hair-cells; 13, outer hair-cells; 14, 16, membrana basilaris; 15, epithelium in the sulcus spiralis; 17, 18, 19, ligamentum spirale; 20, spiral canal below the membrana basilaris.

Lower figure: S T, S T, 5, 5, 7, 7, 8, 8, scala tympani; S V, S V, 9, 9, scala vestibuli; 1, base of the cochlea; 2, apex; 3, 4, central column; 10, 10, 10, 10, ductus cochlearis; 11, branches of the nervus cochlearis; 12, 12, 12, spiral ganglion; 13, 14, limbus laminæ spiralis; 15, membrane of Reissner; 16, epithelium; 17, outer hair-cells; 18, epithelium of the membrana basilaris; 19, nervous filaments; 20, union of the membrana basilaris with the ligamentum spirale; 21, epithelium of the peripheral wall of the ductus cochlearis; 22, 23, membrana tectoria; 24, spiral canal below the membrana basilaris.

internally, by the membrane of Reissner, and, on the other side, by the membrana basilaris.[1] What we thus call the membranous cochlea is divided by the limbus laminæ spiralis and the membrana tectoria into two portions; a triangular canal above, which is the

[1] Some anatomists include this canal in the scala vestibuli. For the sake of clearness, we describe it by itself, as a distinct canal.

larger, and a quadrilateral canal below, between the limbus and membrana tectoria and the membrana basilaris. The quadrilateral canal contains the organ of Corti and various structures of a very complicated character. The relations of these divisions of the cochlea, a knowledge of which is essential to the comprehension of the physiological anatomy of this portion of the auditory apparatus, are shown in Fig. 266.

The membranous cochlea, as described above, follows the spiral course of the cochlea, terminates superiorly in a blind, pointed extremity at the cupola, beyond the hamulus, and is connected below with the saccule of the vestibule by the canalis reuniens. The relations of the different portions of the membranous cochlea to each other and to the scalæ of the cochlea are shown in Fig. 266.

We shall now describe, as possessing the most physiological interest, the liquids of the labyrinth, the distribution and connections of the nerves in the labyrinth, and the organ of Corti.

Liquids of the Labyrinth.—The labyrinth contains a certain quantity of a clear, watery liquid, called the humor of Cotugno, or of Valsalva. A portion of this liquid surrounds the membranous sacs of the vestibule, the semicircular canals, and the membranous cochlea, and this is known as the perilymph of Breschet. Another portion of the liquid fills the membranous labyrinth. This is sometimes called the humor of Scarpa, but it is known more generally as the endolymph of Breschet. The perilymph occupies about one-third of the cavity of the vestibule, of the semicircular canals, and of both scalæ of the cochlea. Both this liquid and the endolymph are clear and watery, becoming somewhat opalescent on the addition of alcohol. The perilymph seems to be secreted by the periosteum lining the osseous labyrinth. As far as we know, the uses of the liquid of the internal ear are to sustain the delicate structures contained in this portion of the auditory apparatus and to conduct sonorous vibrations to the terminal filaments of the auditory nerves and the parts with which they are connected.

Distribution of the Nerves in the Labyrinth.—As the auditory nerves enter the internal auditory meatus, they divide into an anterior, or cochlear, and a posterior, or vestibular branch. The vestibular branch divides into three smaller branches, a superior and anterior, a middle, and a posterior branch. The superior and anterior branch, the largest of the three, is distributed to the utricle, the superior semicircular canal, and the external semicircular canal. The middle branch is distributed to the saccule. The posterior branch passes to the posterior semicircular canal. The nerves distributed to the utricle and saccule penetrate at the points occupied by the otoliths, and the nerves going to the semicircular canals pass to the ampullæ, which also contain otoliths. (See Fig. 264.) In each ampulla, at the point where the nerve enters, is a transverse fold, projecting into the canal and occupying about one-third of its circumference, called the septum transversum.

The nerves terminate in essentially the same way in the sacs of the vestibule and the ampullæ of the semicircular canals. At the points where the nerves enter, in addition to the otoliths, are cells of cylindrical epithelium, of various forms, which pass gradually into the general pavement-epithelium of the cavities. In addition to these cells, are fusiform, nucleated bodies, the free ends of which are provided with hair-like processes, called fila acustica. These are about $\frac{1}{800}$ of an inch in length and are distributed in quite a regular manner around the otoliths. The nerves form an anastomosing plexus beneath the epithelium, and they probably terminate in the fusiform bodies just described as presenting the fila acustica at their free extremities. In the sacs of the vestibule and in the semicircular canals, nerves exist only in the macula acustica and the ampullæ.

The cochlear division of the auditory nerve breaks up into numerous small branches, which pass through foramina at the base of the cochlea, in what is called the tractus spiralis foraminulentus. These follow the axis of the cochlea and pass in their course toward the apex, between the plates of the bony spiral lamina. Between these plates of bone, the dark-bordered nerve-fibres pass each one through a bipolar cell, these cells together forming a spiral ganglion, known as the ganglion of Corti. Beyond this ganglion, the nerves form an anastomosing plexus and finally enter the quadrilateral canal, or the canal of Corti. As they pass into this canal, they suddenly become pale and exceedingly fine, and probably they are connected finally with the organ of Corti, although their exact mode of termination has not yet been determined. The course of the nerve-fibres to their distribution in the cochlea is shown in Fig. 267.

FIG. 267.—*Distribution of the cochlear nerve in the spiral lamina of the cochlea (the cochlea is from the right side and is seen from its antero-inferior part).* (Sappey.)

1, trunk of the cochlear nerve; 2, 2, 2, membranous zone of the spiral lamina; 3, 3, 3, terminal expansion of the cochlear nerve exposed in its whole extent by the removal of the superior plate of the lamina spiralis; 4, orifice of communication of the scala tympani with the scala vestibuli.

Organ of Corti.—Of all the parts contained within the bony labyrinth, the organ of Corti possesses the greatest physiological interest; for it is this organ which is supposed to receive the sonorous vibrations and communicate them directly to the terminal filaments of the auditory nerves. Although this view has not received the support of actual demonstration, it affords an explanation, more or less plausible, of the mechanism of audition, carried to the point of the actual reception of impressions by the nerves. In view of this, it is important to have a clear comprehension of the arrangement of those parts which are supposed to receive the sonorous vibrations; and we shall, for the sake of simplicity, eliminate from our description certain accessory structures, the functions of which are obscure.

In the quadrilateral canal, bathed in the endolymph, throughout its entire spiral course, is an arrangement of pillars, or rods, regular, like the strings of a harp in miniature, which are supposed to repeat the varied vibrations of sound. These are the pillars of Corti.

The structures contained in the quadrilateral canal are so delicate that their investigation presents great difficulty; but the arrangement of the pillars, or rods of Corti is pretty well understood. These pillars are external and internal, with their bases attached to the basilar membrane, and their summits articulated above, so as to form a regular, spiral arcade, enclosing a triangular space, which is bounded below by the basilar membrane. The number of the elements of the organ of Corti is estimated at about 3,500, for the outer, and 5,200, for the inner rods, the proportion of inner rods to the outer being about three to two. The relations of these structures to the membranous labyrinth are seen in Fig. 266. The external pillar is longer, more delicate and rounded, and is also attached to the basilar membrane. The form of the pillars is more exactly shown in Figs. 268 and 269, the latter figure, however, exhibiting other structures which enter into the constitution of the organ of Corti. It will be remarked that a small nucleated body is attached to the base of each pillar. At the summit, where the internal and the external pillars are joined together, is a delicate prolongation, directed outward, which is attached to the covering of the quadrilateral canal.

The above description comprises about all that is definitely known of the arrangement of the pillars, or rods of Corti. They are nearly homogeneous, except when treated with reagents, and are said to be of about the consistence of cartilage. They are closely set together, with very narrow spaces between them, and it is difficult to see how they can be stretched to any considerable degree of tension. The arch is longer at the summit

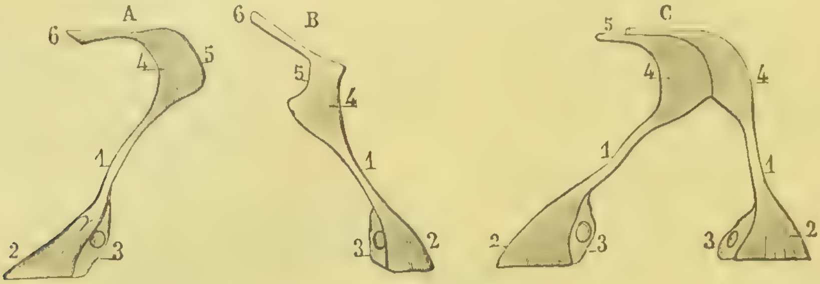


FIG. 268.—*The two pillars of the organ of Corti.* (Sappey.)

A, external pillar of the organ of Corti: 1, body, or middle portion; 2, posterior extremity, or base; 3, cell on its internal side; 4, anterior extremity; 5, convex surface by which it is joined to the internal pillar; 6, prolongation of this extremity.

B, internal pillar of the organ of Corti: 1, body, or middle portion; 2, posterior extremity; 3, cell on its external side; 4, anterior extremity; 5, concave surface by which it is joined to the external pillar; 6, prolongation, lying above the corresponding prolongation of the external pillar.

C, the two pillars of the organ of Corti, united by their anterior extremity, and forming an arcade, the concavity of which presents outward: 1, 1, body, or middle portion of the pillars; 2, 2, posterior extremities; 3, 3, cells attached to the posterior extremities; 4, 4, anterior extremities joined together; 5, terminal prolongation of this extremity.

than at the base of the cochlea, the longest rods, at the summit, measuring about $\frac{1}{200}$ of an inch, and the shortest, at the base, about $\frac{1}{500}$ of an inch. As we before remarked, the relations between the pillars and the terminal filaments of the auditory nerves are not definitely settled.

In addition to the pillars just described, various cellular elements enter into the structure of the organ of Corti. The most important of these are the inner and the outer hair-

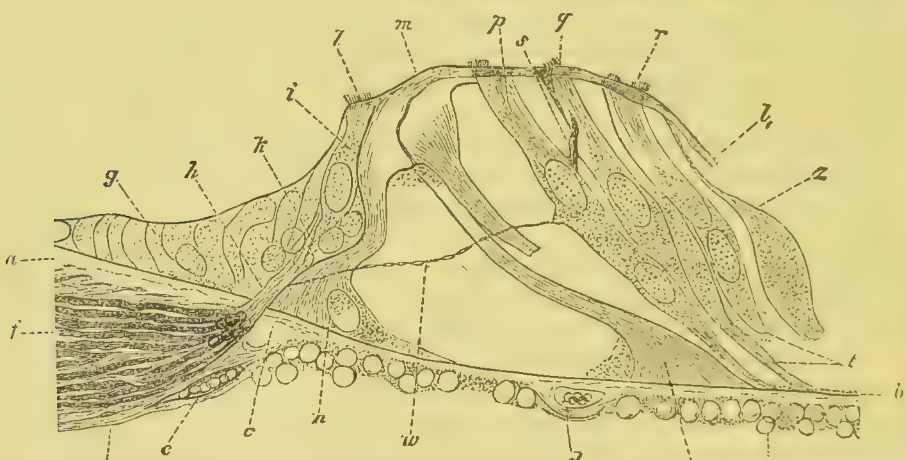


FIG. 269.—*Vertical section of the organ of Corti of the dog; magnified* 800 *diameters.* (Waldeyer.)

a–b, homogeneous layer of the basilar membrane; *v*, tympanic layer, with nuclei, granular cell-protoplasm, and connective tissue; a_1, tympanic lip of the crista spiralis; *c*, thickened portion of the basilar membrane; *d*, spiral vessel; *e*, blood-vessel; *f*, *h*, bundle of nerves; *g*, epithelium; *i*, inner hair-cell, with its basilar process, *k*; *l*, head-plate of the inner pillar; *m*, union of the two pillars; *n*, base of the inner pillar; *o*, base of the outer pillar; *p*, *q*, *r*, outer hair-cells, with traces of the cilia; *t*, bases of two other hair-cells; *z*, Hensen's prop-cell; l–l_1, lamina reticularis; *w*, nerve-fibre passing to the first hair-cell, *p*.

cells. The inner hair-cells are arranged in a single row, and the outer hair-cells, in three rows. Nothing definite is known of the function of these cells. The relations of these parts are shown in Fig. 269, which is rather complex, but, on careful study, gives a good idea of the arrangement of all of the structures which compose the organ of Corti. It is supposed by some anatomists that the filaments of the auditory nerves terminate in the cells above described; but this point is not definitively settled.

Functions of Different Parts of the Internal Ear.

The precise function of the different parts which are found in the internal ear is obscure, notwithstanding the careful researches that have been made into the anatomy and the physiology of the labyrinth. There are several points, however, bearing upon the physiology of this portion of the auditory apparatus, concerning which there can be no doubt:

First, it is certain that impressions of sound are received by the terminal filaments of the auditory nerves and by these nerves are conveyed to the brain.

Second, the functions of the parts composing the external and the middle ear are simply accessory. The sonorous waves are collected by the pavilion and are conveyed by the external meatus to the middle ear; the membrana tympani vibrates under their influence; and they are thus collected, repeated, and transmitted to the internal ear, under the most favorable conditions for producing a proper impression upon the auditory nerves.

In view of these facts, we must look to the functions of semicircular canals and the cochlea, for an elucidation of the problem of the mechanism of the final process of audition; and, in doing this, we come at once to the question of the relative importance of different divisions of the internal ear.

Functions of the Semicircular Canals.—In a memoir presented to the French Academy of Sciences, in 1824, Flourens detailed a number of experiments upon pigeons and rabbits, in which he destroyed different portions of the internal ear. In these experiments, the results of which were very definite, it was shown that destruction of the semicircular canals had apparently no effect upon the sense of hearing, while destruction of the cochlea upon both sides produced complete deafness. In addition, it was observed that destruction of the semicircular canals on both sides was followed by remarkable disturbances in equilibration. The animals could maintain the standing position, but, as soon as they made any movements, "the head commenced to be agitated; and this agitation increasing with the movements of the body, walking and all regular movements finally became impossible, in nearly the same way as when equilibrium and stability of movements are lost after turning several times or violently shaking the head." These observations of Flourens, at least as far as regards the influence of the semicircular canals upon equilibration, have been confirmed by Goltz and are sustained by observations upon the human subject in the condition known as Ménière's disease. In some more recent experiments, however, Boettcher assumes to have demonstrated that the semicircular canals have nothing to do with equilibration; but all of his observations were made upon frogs, in which deficiency of equilibration and of hearing would be very difficult to determine. As far as we can judge from experimental data, it does not seem probable that the nerves directly concerned in audition are distributed to any considerable extent in the semicircular canals. Indeed, the function of these parts is exceedingly obscure; for we can hardly admit, upon purely anatomical grounds, that they are concerned in the discrimination of the direction of sonorous vibrations, an idea which has been advanced by some physiologists.

Functions of the Parts contained in the Cochlea.—There can be no doubt with regard to the capital point in the physiology of the cochlea; namely, that those branches of the auditory nerve which are essential to the sense of hearing and which receive the impressions of sound are distributed mainly in the cochlea. When we come to analyze sonorous impressions, we find that they possess various attributes, such as intensity, quality, and pitch, which have been discussed rather fully under the head of the physics of sound. As far as the terminal filaments of the auditory nerve are concerned, it is evident that the intensity of sound is appreciated in proportion to the power of the impression made upon these nerves, and this point does not demand elaborate discussion. With regard to quality of sound, we have seen that this is due to the form of sonorous vibrations, and that most musical tones are compound, their quality depending largely upon the relative power of the harmonics, partial tones, etc. We have also seen that consonating bodies repeat by influence, not only the actual pitch of tones, but their quality. If there be in the cochlea an anatomical arrangement of rods or fibres by which the sonorous vibrations, conveyed to the ear by the atmosphere, are repeated, there is reason to believe that the quality, as well as the pitch, is reproduced. Narrowing down the question, then, to its most interesting and important point, viz., the appreciation of differences in the pitch of musical tones, we inquire whether there be in the cochlea any arrangement by which the pitch can be repeated. This inquiry can only be answered by a study of the anatomical arrangement of the structures connected with the terminal filaments of the nerves, and by the application of physical laws.

The arrangement of the rods which enter into the structure of the organ of Corti has afforded a theoretical explanation of the final mechanism of the appreciation of pitch. Until we come to the internal ear, the action of different portions of the auditory apparatus is simply to conduct and repeat sonorous vibrations; and the sole function of these accessory parts, aside from the protection of the organs, is to convey the vibrations to the terminal nervous filaments. Whatever be the functions of the membrana tympani in repeating sounds by influence, it is certain that this membrane possesses no true auditory nerves, and that the auditory nerves only are capable of receiving impressions of sound. Thus, hearing, and even the appreciation of pitch, is not necessarily lost after destruction of the membrana tympani; and, if sonorous vibrations reach the auditory nerves, they will be appreciated and appreciated correctly. With this point clearly understood, we are prepared to study the probable functions of the organ of Corti.

When we consider the organ of Corti, with its eight thousand or more rods of different lengths arranged with a certain degree of regularity, a number more than sufficient to represent all the tones of the musical scale, we are not surprised that eminent physiologists regard them as capable of repeating all the shades of tone heard in music. Helmholtz formularizes this idea in the theory that tones conveyed to the cochlea throw into vibration those elements of the organ of Corti which are tuned, so to speak, in unison with them. According to this hypothesis, the rods of Corti constitute a harp of several thousand strings, played upon, as it were, by the sonorous vibrations.

It would be difficult to imagine any thing more satisfactory and simple than such an hypothesis as we have just quoted. Attention and education enable persons endowed with what is called a musical ear to discriminate between different tones with great accuracy. Experiments have shown that the situation of the actual appreciation of tones may be restricted to the cochlea; and, in the cochlea, the only anatomical arrangement, as far as we know, which points toward an appreciation of the pitch of different tones is that of the rods of Corti. Still, it must be remembered that the cochlea is so situated as to be removed from the possibility of experimental investigation to prove the theory; and we must carefully study the anatomical arrangement of the parts and the possible application of physical laws to the supposed vibration of the rods.

Viewing the question from its anatomical aspect, it is by no means certain that the rods of Corti are so attached and stretched that they are capable of separate and individual vibrations. It has not been demonstrated that certain of these rods vibrate under the influence of certain tones or that they are tuned in accord with certain tones. Hensen, who has written elaborately upon the very question under consideration, denies the accuracy of the theory of Helmholtz, basing his opinion upon the anatomical arrangement of the rods of Corti, and he assumes that it is a physical impossibility for the different rods to vibrate individually, and that it is not certain that they are tuned in accord with different tones. Hensen makes, upon this point, the following statement:

"It is now my conviction, that by the hypothesis 'more and more corroborated' that the fibres of Corti constitute the organ of the labyrinth tuned to the appreciation of tones, our comprehension and the investigation of the internal ear have taken a false direction.

"I assert, next, that the rods of Corti cannot play the important part in the appreciation of tones, which has been attributed to them in the hypothesis of Helmholtz."

It is pretty evident that, although the theory of Helmholtz is undoubtedly the only one affording any reasonable explanation of the appreciation of tones, it lacks positive anatomical confirmation. And, farthermore, we do not even know the anatomical connections between the rods of Corti and the filaments of the auditory nerves.

In view of the considerations just given, we have simply recited the theory of Du Verney, Le Cat, and Helmholtz, as one which may or may not be sustained hereafter by more exact researches; but at present it must be acknowledged that there is no more satisfactory explanation of the mechanism of the final appreciation of musical tones.

Summary of the Mechanism of Audition.

The waves of sound are simply collected by the pavilion of the ear and are conveyed, through the external meatus, to the membrana tympani. The membrana tympani, a delicate, rounded, concave membrane, receives these waves and is thrown into vibration.

The arrangement of the bones and muscles of the middle ear admits of variations in the tension of the membrana tympani. By increasing the tension of this membrane, the ear may be rendered insensible to grave sounds, while high-pitched sounds become more intense; and, in cases of voluntary tension, the limit of perception of high tones may be greatly extended. The membrana tympani obeys the laws of consonance and vibrates strongly under the influence of sounds in unison or in harmony with its fundamental tone, returning, in this way, not only the pitch, but the quality of tones and combinations of tones in harmony. Destruction of the membrane does not necessarily of itself destroy hearing, or even the appreciation of tones, for the impressions may be conducted to the cochlea by the chain of ossicles.

The arrangement of the ossicles and muscles of the middle ear is such that contraction of the tensor tympani renders the articulations firm, tightens the little ligaments, and presses the stapes against the liquid of the labyrinth, so that the chain resembles, in its action, a solid and continuous bony rod. By this arrangement, the sonorous vibrations are conducted to the labyrinth with very little loss of intensity.

The cavity of the tympanum is filled with air, communicates with the mastoid cells, and with the pharynx by means of the Eustachian tube; and, by this means, the pressure of air in its interior is regulated. The labyrinth, consisting of the vestibule, semicircular canals, and cochlea, is filled with liquid, and the different cavities communicate with each other. The vibrations, repeated by the membrana tympani, are conveyed by the chain of bones to the liquid of the labyrinth, and by it to the terminal filaments of the auditory nerves.

The vestibule and semicircular canals seem to possess much less importance in the appreciation of sound than the cochlea. In the cochlea, throughout the entire extent of the spiral canal, is the organ of Corti, presenting, among other structures, about 8,700 rods, varying in length, called the rods of Corti. But little is known of the anatomical relations between the auditory nerves and the organ of Corti; still, it is thought, as a matter of pure theory, that the rods of Corti are tuned in unison with different tones, that they repeat the tones conveyed to the cochlea, and that we are thus enabled to distinguish the different tones in music.

We have no very definite knowledge of the functions of the cells of the organ of Corti, of the otoliths, and of various other structures in the auditory apparatus. Sounds may be conducted to the auditory nerves through the bones of the head and the Eustachian tube, as is shown by the simple and familiar experiment of placing a tuning-fork in vibration in contact with the head or between the teeth.

CHAPTER XXVI.

ORGANS AND ELEMENTS OF GENERATION.

General considerations—Sexual generation—Spontaneous generation (so called)—Female organs of generation—General arrangement of the female organs—External and internal organs—The ovaries—Development of the Graafian follicles—The parovarium—The uterus—The Fallopian tubes—Structure of the ovum—Vitelline membrane—Vitellus—Germinal vesicle and germinal spot—Discharge of the ovum—Puberty and menstruation—Description of a menstrual period—Characters of the menstrual flow—Changes in the uterine mucous membrane during menstruation—Changes in the Graafian follicle after its rupture (corpus luteum)—The testicles—Tunica vaginalis—Tunica albuginea—Tunica vasculosa—Seminiferous tubes—Epididymis—Vas deferens—Vesiculæ seminales—Prostate—Glands of the urethra—Semen—Secretions mixed with the products of the testicles—Spermatozoids—Development of the spermatozoids—Seminal fluid in advanced age.

A REVIEW of the physiological processes which we have thus far studied shows that the functions of the perfected organism are divided into two great classes:

The first class of functions may be grouped under the general head of nutrition, taken in its widest sense. Nutrition is common to animal and vegetable life, and this is sometimes called a vegetative process.

The study of nutrition involves the following considerations: First, the blood, which is the great nutritive fluid, contained in the innumerable vessels which penetrate nearly all of the tissues and organs of the body and are connected with the system of lymphatic and lacteal vessels. Second, the process by which the blood is circulated, sent by the heart to all parts in the capillary system, used by the tissues for their nutrition, then losing oxygen, gaining carbonic acid, and being returned by the veins. Third, respiration, the blood being freed from carbonic acid and getting a new supply of oxygen in the lungs, by which it is rendered capable of again circulating through the general system. Fourth, as the blood, in its passage through the capillary vessels, not only loses oxygen, but is more or less impoverished by the assimilation of its nutritive constituents by the tissues, it is necessary to keep it up to the proper nutritive standard; and this is effected by alimentation, digestion, and absorption. Fifth, we have certain secretions, necessary to the above-mentioned processes; and the products of physiological waste or decay of the tissues are removed by excretion. Sixth, the processes of vegetative life involve the production of heat and are regulated and coördinated by the nervous system.

The second class of functions relates to animal life, and these are called the functions of relation. In this class, are included movements, voice and speech, the functions of the cerebro-spinal nervous system, and the operation of the special senses.

In studying the processes of nutrition of the general system, we observe that certain constituents of the organism, which contain nitrogen and are exclusively of organic origin, have the property, in the living body, of self-regeneration; *i. e.*, when these parts are brought in contact with nutritive matter in proper form, as it exists in the blood, this matter is appropriated and transformed into the substance of each tissue and organ. It is in this way that, during adult life, the different parts of the organism are maintained in a tolerably uniform condition. In the absence of an exact knowledge of the cause and nature of these assimilative processes, we call them vital; which term is applied to a constant property of living, organized parts. Physiologists have ascertained that each tissue and organ of the body possesses one or more characteristic organic nitrogenized constituents which are possessed of this so-called vital property. But, at the same time, it is always observed that the organic nitrogenized constituents of the organism are combined most intimately with a tolerably definite quantity of inorganic matter, which latter regulates, to a certain extent, nutritive processes, and constitutes, also, an important component part of the tissues. It is observed, in addition, that, during early life, when the system is proceeding toward its perfect development by growth, the proportion of inorganic matter is less than in the adult, and that the process of nutrition is then at its maximum of activity, the regeneration being superior to the waste. During the adult period, repair and physiological decay are nearly balanced; but, in the decline of life, there seems to be a gradual accumulation of inorganic matter, and this continues until the so-called vital properties of some important organ become so feeble that its functions cease, and we have physiological death. This regeneration of the tissues is a necessary consequence of the constant waste or decay of every part of the organism, resulting in a change of constituents into effete matters, which are discharged; there being, during life, a constant waste and repair. If no new matter be introduced as food, the system wastes to a point which is incompatible with life, and death results from inanition.

With some very insignificant exceptions, we cannot conceive that living tissues exist in an absolutely stationary condition. The organized parts of the body are undergoing constant molecular destruction and repair. Again, the so-called vital properties of the tissues, which involve self-regeneration, seem to have certain limits. We cannot introduce nutritive matter in sufficient quantity to produce growth beyond a certain point, although we may limit development and growth by deficient supply. When we ask why the organs develop with fixed regularity, why, when an occasional excess of nutritive matter is presented, this excess is not used, we must confess our ignorance or say that the parts are endowed with vital properties. We also find, to come to the most important point of this discussion, that, however carefully we may supply nutritive matter to the system, we cannot arrest the gradual enfeeblement of the assimilative powers of the tissues, which occurs in old age. In short, as we cannot conceive of a living tissue without decay and regeneration of its substance, so it is impossible for the organism to last for an indefinite period. A necessary, invariable, and inevitable consequence of individual life is death. The constant molecular death—if we can apply this term to the transformation of living into effete matter—of every tissue of the body is always, in the end, superior to the power of repair. There seems, indeed, to be an antagonism of processes during life; a view which was so fully adopted by Bichat, that it led to his celebrated definition of life; "the *ensemble* of functions which resist death." Although death is thus inevitable, and, in the circulation of material in Nature, the organic parts of the body become changed in the arrangement of their ultimate elements and appropriated by the vegetable kingdom, during adult life, certain anatomical elements, male and female, are formed in the human subject, which, when they come together under proper conditions, develop into new beings, which pass through the same course of existence as the parents. By the concourse of two beings, new organisms come into life, which perpetuate existence and preserve species. The function by which this is accomplished is called generation, or reproduction.

In our study of generation, we shall confine ourselves as closely as possible to the process as it takes place in the human subject. There are many considerations of great interest connected with the generation of the lowest orders of animal organization, among the most prominent of which is the question of so-called spontaneous generation. While this may have a certain bearing upon the genesis of anatomical elements, it has little or nothing to do with the development of the fecundated human ovum, and will, therefore, receive little more than an incidental consideration. For similar reasons, we shall not engage in a discussion of the development-theory applied to the origin of species, which is exciting so much controversy at the present day, nor shall we treat of generation in the lower animals, except to illustrate the history of development in man.

The study of human generation will naturally assume the following course: First, the female organs of generation and the formation of the female element, the ovum; second, the discharge of the ovum and the phenomena which attend this process; third, the male organs and the development and discharge of the male elements, the spermatozoids; fourth, the union of the two elements of generation, or fecundation; fifth, the development of the fecundated ovum into the fœtus at term; sixth, the development of the body after birth and at different ages, or stages of existence; finally, the natural cessation of the so-called vital functions, or physiological death.

Sexual Generation.

Before we describe the actual phenomena of sexual generation, as they are observed in man and the mammalia, it will be interesting to note some of the salient points in the history of our knowledge of this process in the inferior animals. This we can do, without exceeding the limits we have laid down in our general remarks.

In the history of sexual generation, there seems to have been a limiting line between the production of animals from preëxisting organisms and of those produced in some unknown manner, or, as it has been said, spontaneously. This line of distinction has always receded toward organisms lower and lower in the scale of being, with our advance in positive knowledge. The ancients understood that the higher animals required for their production a concourse of the sexes; but they thought that many fishes, reptiles, insects, worms, etc., were produced spontaneously. Indeed, with the limited knowledge of natural history possessed by Aristotle and those who succeeded him for many hundred years, the classes of animals said to be produced spontaneously represented simply those, the generation of which was not understood. But, as the habits of many animals became better understood, more and more of them were observed to lay eggs, which were found to undergo development.

Dating from Aristotle, who lived between three and four hundred years B. C., it was nearly two thousand years before any thing was known of the generation of insects; the difficulty here being that the young are first in a larval state and bear no resemblance to the parents. Anterior to the experiments of Redi, it was thought that certain organic matters in course of putrefaction developed living organisms, as maggots in meat and the larvæ in cheese.

We refer to the experiments of Redi, made about the year 1668, for the reason that these mark an era in our knowledge of the process of generation. This observer, noting that flies frequently lighted upon meat when it was exposed, simply protected it by gauze and found that no maggots were developed, while other pieces of meat, placed under the same conditions, except that the flies had free access to them, developed maggots in great numbers. By this simple experiment, Redi showed that the maggots in putrefying meat were produced by insects and not by the meat; but it remained for Swammerdam and Vallisneri to study the metamorphoses of insects, and to show how the eggs were developed, first into sexless larvæ, and finally into perfect beings resembling the parents. It is curious to note the condition of science anterior to Redi and Vallisneri and compare it with the ideas that are current at the present day. When maggots appeared in putrefying meat, they were thought to be produced by a spontaneous aggregation of organic particles, simply because observers knew of no other way in which these beings could come into existence. Now, the advocates of spontaneous generation have the same ideas as those advanced anterior to 1668; but, in the place of meat, they have organic infusions, and for maggots, they substitute infusorial animalcules. It is possible that the discussion of the question then was as energetic as it is now; but the positive advances in a knowledge of the generation of insects has swept away the memory of such discussions, if they existed, as future advances may possibly cause many of the controversial writings of the present day to pass into oblivion.

For a time after the researches to which we have just alluded had taken their place in the history of science, there was little written about spontaneous generation. Redi had satisfactorily described the mode of generation of many of the entozoa, the origin of which had been obscure; Harvey had enunciated, in substance, his famous axiom, "*omne animal ex ovo;*" Regnerus de Graaf had described, in the ovaries, the vesicles which have since borne his name; and the knowledge of ovulation and development began to make definite progress, the important fact having been ascertained, that viviparous, as well as oviparous animals, are produced from ova.

With the discovery, by Leeuwenhoek, of living beings in water, called by him animalcules, but since known as infusoria, a new problem was presented to students of natural history. Here were animal organisms, so small as to be invisible to the naked eye, existing in great variety and in infinite numbers, the mode of generation of which was not understood. As these organisms were studied more closely, their multiplication by segmentation and by budding became known, and these have since been described as processes of generation peculiar to some of the lower orders of beings; but, at the same time, some writers revived the theory of spontaneous generation, to account for the original appearance of animalcules in water, and this idea has its advocates at the present day. If, however, we follow out the history of the spontaneous-generation theory, we find that the different epochs have repeated themselves; that the theory took its origin from an ignorance of the mode of generation of organisms quite high in the scale of being; that the progress of exact knowledge gradually restricted the theory to lower and lower organisms, until, by this rigid process, it became extinct, simply from want of material; that its application to entozoa was eliminated in the same way; that it was revived by the discovery of infusoria; and that now its limits have been restricted by positive advances in knowledge, it being demonstrated, by Balbiani and others, that many varieties of infusoria present the phenomena of sexual generation.

Of the advocates of spontaneous generation within a comparatively recent period, perhaps the most prominent has been Pouchet; but modern researches have shown pretty clearly that the infusoria produced in organic infusions are due, in all probability, to the introduction of ova or spores floating in the air, which are developed when they meet with proper conditions of heat and moisture. In numerous experiments by different observers, which it is not necessary to cite in detail, it appeared that, when organic infusions had been exposed to a degree of heat sufficient to destroy germs, and the introduction of new germs from the air was prevented, no infusoria were developed; and this was the case when air was admitted to the infusions, care being taken to pass the air through heated tubes or sulphuric acid, so as to destroy all organic matter. The present aspect of the question of spontaneous generation is the following:

First, it is reduced to the very lowest orders of infusoria, such as vibriones and bacteria, which simply present movement, have no distinguishable internal structure, and are exceedingly minute.

Second, the question is discussed as to what degree of temperature and length of exposure to heat are necessary in order to destroy preëxisting germs in organic infusions; for the idea that living organisms ever result from an aggregation of inorganic particles has been generally abandoned, and the so-called spontaneous production of animals has been reduced to a coming together of organic molecules.

It is at once apparent to the rigidly scientific mind that the second division of the question presents great difficulties in the way of its positive solution. It is granted, for example, that vibriones and bacteria are living, animal organisms. It is proposed by the advocates of the theory of spontaneous generation, that these beings arise without preëxisting germs, by an aggregation of organic particles. The opponents of this view assert that, when the air admitted to organic infusions is freed from germs or organic particles, and when the organic infusions are subjected to a high temperature for a time sufficient to destroy all possible preëxisting germs, no generation of infusoria can take place.

Now, what degree of temperature is required, what is the duration of exposure to heat necessary to destroy germs, and how are the limits of these conditions to be ascertained? The only answer to this question lies in the experimental test. When infusoria make their appearance in solutions that have been exposed to heat and protected from the entrance of germs, it is said that the heat has not been sufficiently high or the exposure has been of too short duration. When infusoria do not appear, the conditions are assumed to have been fulfilled. This mode of reasoning assumes the fact, from the beginning, that there is no such thing as spontaneous generation. Suppose, now, we start with the contrary assumption, that there may be spontaneous generation in an organic infusion. We admit to such an infusion, air, carefully purified from germs, which is logically an essential experimental condition; we have previously exposed the infusion to a high temperature for a certain period. Under these conditions, no infusoria appear. It may then be assumed that the heat has destroyed the properties of the organic molecules, so that they cannot come together and generate new beings.

Under these circumstances, all that we can do is to argue logically from such facts as have been positively established, and to take the most reasonable view of other points, that are not as yet capable of satisfactory and definite explanation.

We shall assume that it has been demonstrated, beyond a reasonable doubt, that, in organic infusions, subjected to a temperature somewhat above that of boiling water, and supplied with air that has been effectually deprived of organic matter, ova, spores, or whatever it may be, no living organisms make their appearance so long as these experimental conditions are maintained. We also assume that simple boiling, at 212° Fahr., does not necessarily destroy all germs, which excludes experiments made in this way. This reduces the question to a single, simple point: In infusions in which the organic matter has not been destroyed by heat, do the living organisms come from a spontaneous aggregation of organic molecules, or are they the result of the development of ova?

In the case of the very lowest organisms making their appearance under these conditions, they are themselves so small, that it would be reasonable to suppose that we might be unable to see the ova, assuming that they exist. The organic particles that are supposed to come together spontaneously are also invisible, even under the highest magnifying powers at our command. If we come to an exact definition of the term spontaneous, we may say that it means an action "arising or existing from natural inclination, disposition, or tendency, or without external cause" (Worcester). With this definition, the statement that a living organism is generated spontaneously can only mean that there is no cause that can be assigned for its production. In point of fact, we simply acknowledge that the mode and cause of generation of certain infusoria are unknown, and the history of our knowledge of generation shows that the term spontaneous generation has always been applied to the production of beings in a manner that is incapable of satisfactory explanation. What we actually know of the mode of generation of animal organisms teaches us that all beings are produced and multiplied by ova, or by processes of segmentation or budding of preëxisting organisms; and our knowledge of these processes now extends to all except the most minute infusoria, which have no apparent structure. We know, also, that such organisms may develop in pure water from particles floating in the atmosphere; and that particles in the air, singly invisible, may be developed into infusoria that are quite highly organized. If we reason that the products of so-called spontaneous generation are formed by the fortuitous aggregation of organic molecules, we assume a fact of which we have no other example in Nature; and we assume, also, that such an aggregation of particles produces beings of a definite and uniform character. For such a supposition, we have no basis in analogy. If, on the other hand, we regard these low orders of beings as produced by the development of invisible germs, which have found favorable conditions of heat and moisture, we rest upon a basis of reasonable analogy, and we merely confess that this is a form of generation, the processes of which are not as yet capable of demonstration.

As the only true philosophic view to take of the question, we shall assume, in common with nearly all modern writers upon physiology, that there is no such thing in Nature as spontaneous generation; admitting that the exact mode of production of some of the infusoria, lowest in the scale of being, is not understood.

Female Organs of Generation.

An accurate knowledge of certain points in the anatomy of the female organs of generation is essential to the comprehension of the most important of the processes of reproduction. Following a fruitful intercourse of the sexes, the function, as regards the male, ceases with the comparatively simple process of penetration of the male element through the protective covering of the ovum and its fusion with the female element. The fecundated ovum then passes through certain changes, which are the first processes of its development, forms its attachments to the body of the mother, continues its development, materials being derived from the mother, is nourished and grows, until the fœtus at term is brought into the world. An exact knowledge of the mechanism of these complicated processes can only be obtained after a careful study of the anatomy of the female organs. We must know precisely how the ovum is developed in the ovary and how it is discharged; how, after its discharge, it is received by the oviduct and carried to the uterus; if fecundation do not take place, there is nothing more to study, as the ovum is lost; but, as the fecundated ovum must form certain attachments within the uterus, we must be acquainted with the anatomy of this organ, before we can comprehend its development. Again, we have to study the phenomena which attend the discharge of ova, and the changes which take place in the ovaries, anterior to, during, and subsequent to ovulation. It will not be essential for us to study very closely the anatomy of the external parts, as these are only concerned in sexual intercourse and in parturition; which latter, though a purely physiological process, forms the greatest part of the science of obstetrics, is considered elaborately in treatises on this subject, and is not usually treated of, to any great extent, in works upon physiology.

The female organs of generation are divided anatomically into internal and external. The external organs are the vulva, the adjacent parts, and the vagina; the internal organs are the uterus, Fallopian tubes, and ovaries. When we come to study the functions of the internal parts, we shall see that the ovaries are the true female organs, in which, and in which alone, the female element can be produced. The Fallopian tubes and the uterus are accessory in their functions, the female element (the ovum) passing through the Fallopian tubes to the uterus, where it forms the attachments to the body of the mother which are essential to its nourishment and full development after fecundation.

Before we proceed to study the structure of any of the female organs, it is important to have a clear idea of the general arrangement and the relations of these parts; for, without this, we shall be constantly in the dark as to the bearing of certain important anatomical points that have been brought forward within the last few years.

The vagina has a direction, slightly curved anteriorly, which is nearly coincident with the axis of the outlet, or the inferior strait of the pelvis. Projecting into the vagina, at its upper extremity, is the lower part of the neck of the uterus. The uterus extends from the vagina nearly to the brim of the pelvis. It is situated between the bladder and the rectum, and has an antero-posterior inclination, when the bladder is moderately distended, which brings its axis nearly coincident with that of the superior strait of the pelvis.[1] Supposing the body to be erect, the angle of the uterus with the perpendicular would be about forty-five degrees. These details with regard to the position of the uterus

[1] The statements given above, with regard to the position of the uterus, are very general. The uterus is exceedingly movable antero-posteriorly, and the direction of its axis is largely dependent upon the condition of the other pelvic organs. When the bladder is distended, the fundus is moved upward; and, when the bladder is empty, the axis of the uterus may be inclined forward so as to become nearly horizontal.

are essential to a comprehension of the situation and relations of the ovaries and Fallopian tubes.

The uterus is held in place by ligaments, certain of which are formed of folds of the peritoneum. The anterior ligament is reflected from the anterior surface to the bladder; the posterior ligament extends from the posterior surface to the rectum; the round ligaments extend from the upper angle of the uterus, on either side, between the folds of the broad ligament and through the inguinal canal, to the symphysis pubis; the broad ligaments, which extend from the sides of the uterus to the walls of the pelvis, are the most interesting of all, as they lodge the ovaries and the Fallopian tubes.

If we imagine the uterus, occupying, as it does, the upper part of the pelvis, and remember its angle of inclination, it is evident that it, with the broad ligaments, must partially divide the pelvis into two portions; and these ligaments, which are formed of a double fold of peritoneum, present a superior, or posterior surface, and an inferior, or anterior surface. The superior, or anterior border of this fold is occupied by the Fallopian tubes, the peritoneum constituting their outer coat. Laterally, at the free extremities of the tubes, the peritoneum ceases, and there is an actual opening of each Fallopian tube into the peritoneal cavity. Attached to the broad ligament and projecting upon its posterior surface, is the ovary. This little, almond-shaped body is connected with the fibrous tissue between the two layers of the ligament, and has no proper peritoneal investment; so that it is actually within the peritoneal cavity. If we look at the ovary from the front, we simply see the rounded prominence which marks the point of its attachment to the broad ligament; but, if we look from behind, the projecting surface is seen, and we

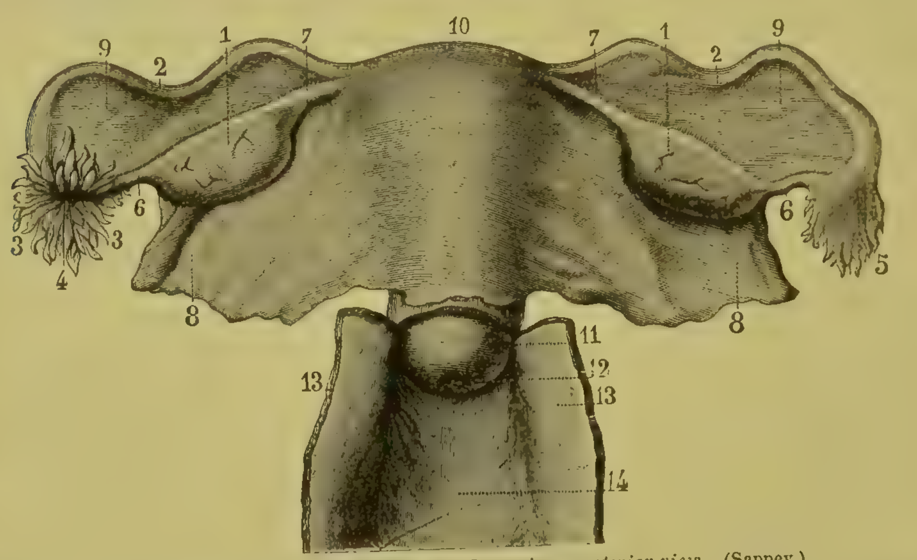


FIG. 270.—*Uterus, Fallopian tubes, and ovaries; posterior view.* (Sappey.)
1, 1, ovaries; 2, 2, Fallopian tubes; 3, 3, fimbriated extremity of the left Fallopian tube seen from its concavity; 4, opening of the left tube; 5, fimbriated extremity of the right tube, posterior view; 6, 6, fimbriæ which attach the extremity of each tube to the ovary; 7, 7, ligaments of the ovary; 8, 8, 9, 9, broad ligaments; 10, uterus; 11, cervix uteri; 12, os uteri; 13, 13, 14, vagina.

have a distinct ring of demarcation at the base, which indicates where the tessellated, serous epithelium ceases, and where the proper columnar epithelium of the ovary begins. If a vesicle should rupture upon the surface of the ovary, its contents might thus be taken up by the Fallopian tube and be carried to the uterus. Each ovary is attached to the uterus by a ligament, lying just beneath the peritoneum, called the ligament of the ovary. This ligament is composed of non-striated muscular fibres. Between the folds of the broad ligament, are the following structures: the round ligament of the uterus, blood-vessels, nerves, and a thin layer of non-striated muscular fibres, continuous with the superficial muscular fibres of the uterus.

We are now prepared to study Fig. 270, which shows the general arrangement of these parts, viewed from behind. A portion of the figure which, in the original, shows the external parts, is cut off, to avoid complicating our description. A careful examination of Fig. 270 will give a general idea of the relations of the different parts and enable us to study intelligently their minute anatomy.

The Ovaries.—The situation of these bodies has already been indicated. Attached, as they are, to the broad ligament, and projecting from its posterior surface, they lie nearly horizontally in the pelvic cavity, on either side of the uterus. They are of a whitish color, and their form is ovoid and flattened, with the anterior border, sometimes called the base, attached to the broad ligament. If we closely examine their mode of connection with the broad ligament, it is seen that, at the margin of the attached surface of the ovary, the posterior layer of the ligament ceases, and that the fibrous stroma of the medullary portion of the ovary is continuous with the fibrous tissue lying between the two layers. It is at this portion of the ovary, called the hilum, that the vessels penetrate, to be distributed in its substance.

Each ovary is about an inch and a half in length, half an inch in thickness, and three-quarters of an inch in width at its broadest portion. The outer extremity is somewhat rounded and is attached to one of the fimbriæ of the Fallopian tube. The inner extremity is more pointed and is attached to the side of the uterus by means of the ligament of the ovary. This ligament is shown in Fig. 270 (7, 7). It is a rounded cord, composed of non-striated muscular fibres spread out upon the attached extremity of the ovary and the posterior surface of the uterus, and is covered by peritoneum. The weight of each ovary is from sixty to one hundred grains, and these organs are largest in the adult virgin. Its attached border is called the hilum; and, at this portion, the vessels and nerves penetrate. The surface is marked by rounded, translucent elevations, produced by distended Graafian follicles; and we frequently see here little cicatrices, indicating the situation of ruptured follicles. We may also see, between the distended follicles, corpora lutea in various stages of atrophy.

Within the last few years, anatomical researches have shown that the surface of the ovaries does not present the appearance of a continuation of the peritoneum. At the base, is a distinct line, surrounding the hilum, which indicates where the peritoneum ceases and where the proper epithelial covering of the ovary begins; and there is a well-marked and abrupt distinction between the tessellated epithelium of the serous surface and the layer of cylindrical cells covering the ovary itself. This peculiarity has led to the idea that the ovary is really covered by a mucous membrane. Indeed, there seems to be little difference between the cells covering the ovaries and those lining the Fallopian tubes, except that the latter are provided with cilia.

Most anatomists describe a proper fibrous membrane investing the ovaries, which they call the tunica albuginea, and which is compared to the fibrous covering of the testes. This, however, is not a proper term. Sappey denies the existence of a tunica albuginea; and, indeed, in the sense in which it was formerly described, such a membrane cannot be demonstrated. On making a section of the ovary, it is readily seen by the naked eye that the organ is composed of two distinct structures; a cortical substance, formerly called the tunica albuginea, which is about $\frac{1}{25}$ of an inch in thickness, and a medullary substance, containing a large number of blood-vessels. The cortical substance alone contains the Graafian follicles. The external layer of this may be a little denser than the deeper portion, but there is no distinct fibrous membrane.

The structure of the cortical substance of the ovary is very simple. It consists of connective tissue in several layers, the fibres of which are continuous with the looser fibres of the medullary portion. In the substance of this layer, are embedded the ova, enclosed in the sacs called Graafian follicles. This layer contains a few blood-vessels, coming from the medullary portion, which surround the follicles.

The medullary portion of the ovary is exceedingly vascular and is composed of numerous small bands, or trabeculæ of connective tissue, with smooth muscular fibres. The blood-vessels, which penetrate at the hilum, are large and convoluted, especially at the hilum itself, where there is a mass of convoluted veins, forming a sort of vascular bulb, which has been described particularly by Rouget. In the medullary portion of the ovary, which is sometimes called the vascular zone, the muscular fibres follow the vessels, in the form of muscular sheaths. According to Rouget, the mass of vessels at the hilum constitutes a true erectile organ.

In addition to the blood-vessels, the ovary receives nerves from the spermatic plexus of the sympathetic, the exact mode of termination of which has not been ascertained. Lymphatics have also been demonstrated at the hilum.

Graafian Follicles.—These vesicles, or follicles, were described and figured by De Graaf and are known by his name. They contain the ova, undergo a series of interesting changes, enlarge, approach the surface of the ovary, and finally are ruptured, discharging their contents into the fimbriated extremity of the Fallopian tube.

It was formerly supposed that the smallest Graafian follicles were situated deeply in the medullary portion of the ovaries, approaching the surface gradually, as they became larger; but it is now known that they are developed exclusively in the cortical substance. If, indeed, we examine the ovary at any period of life, we find no follicles properly in the medullary substance; but a few of the larger may project downward, so as to encroach somewhat upon it, being actually of a diameter greater than the thickness of the cortex.

The earlier anatomists supposed that the Graafian follicles were few in number, fifteen or twenty, but they counted those only that were readily seen with the naked eye. When, however, it was calculated that ova might be discharged every month during a period of about forty years, it became evident that the follicles must either be quite numerous or become successively and constantly developed. This led some anatomists, who believed that, at the age of puberty, the ovaries contained, either partially or fully developed, all the follicles that ever existed in these organs, to increase their estimates of the number of follicles. Sappey, from a series of careful observations on this point, puts the number of follicles at from 600,000 to 700,000. We cannot but regard this estimate as very much exaggerated. According to the table of measurements given by Waldeyer, the primordial follicles in the human embryo, at the seventh month, measure from $\frac{1}{800}$ to $\frac{1}{250}$ of an inch, and the primordial ova, from $\frac{1}{1875}$ to $\frac{1}{1000}$ of an inch. From what has been written on this point, it seems difficult, if not impossible, to give an approximation, even, of the number of follicles in the ovaries, but there certainly must be several thousands, many of which may never become fully developed.

Within the last few years, very important advances have been made in our knowledge of the mode of development of the ova and ovaries, which will be more fully considered hereafter; but we must here refer to these points briefly, in order to give a clear idea of the relations of the Graafian follicles, in the different forms which they present under varied conditions of development.

The ovary appears, particularly from observations upon the development of the chick, very early in embryonic life, in the form of a cellular outgrowth from the Wolffian body. Most of its cells are small, but, as early as the fourth or fifth day, some of them are to be distinguished by their large size, their rounded form, and the presence of a large nucleus. These cells are supposed to be primordial ova. In the process of development of the ovary, some of the peripheral cells penetrate in the form of tubes (the so-called ovarian tubes) and, at the same time, delicate processes, formed of connective tissue and blood-vessels, extend from the fibrous stroma underlying the epithelium and enclose collections of cells. It is probable that we have these two modes of formation of follicles; one, by the penetration of epithelial tubes from the surface, which become constricted and divided off into closed cavities, and the other, by the extension of fibrous processes from below, which enclose little collections of cells. By both of these processes, little cavities are formed, which contain a number of cells. In each of these cavities, we observe a single, large, rounded cell, with a large nucleus, this cell being a primordial ovum; and, in addition, we have in the same cavity, other cells, which are the cells of the Graafian follicle. The exact nature of the processes we have just described has been studied in the fowl, but it is probable that the same kind of development occurs in mammalia and in the human female.

From birth until just before the age of puberty, the cortical substance of the ovary contains thousands of what are termed primordial follicles, enclosing the primordial ova; and it is probable that, after the ovaries are fully developed at birth, no additional ova or Graafian follicles make their appearance. The prevailing idea is, indeed, that the great majority of these never arrive at maturity, and that they undergo atrophy at vari-

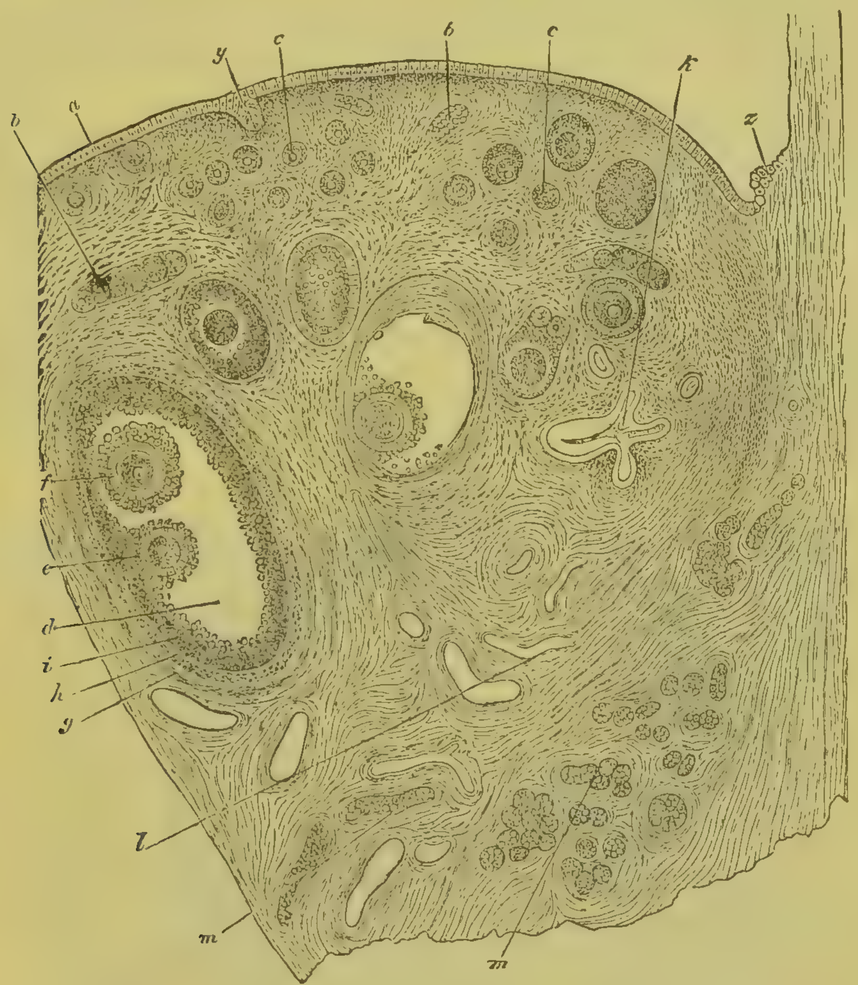


FIG. 271.—*Portion of a sagittal section of the ovary of an old bitch* (Waldeyer.)
a, ovarian epithelium; *b*, *b*, ovarian tubes; *c*, *c*, younger follicles; *d*, older follicle; *e*, discus proligerus, with the ovum; *f*, epithelium of a second ovum in the same follicle; *g*, fibrous coat of the follicle; *h*, proper coat of the follicle; *i*, epithelium of the follicle (membrana granulosa); *k*, collapsed, atrophied follicle; *l*, blood-vessels; *m*, *m*, cell-tubes of the parovarium, divided longitudinally and transversely; *y*, tubular depression of the ovarian epithelium in the tissue of the ovary; *z*, beginning of the ovarian epithelium close to the lower border of the ovary.

ous stages of their development. According to the table of measurements given by Waldeyer, the primordial follicles of the human embryo, at the seventh month, are from about $\frac{1}{800}$ to $\frac{1}{250}$ of an inch in diameter, and the primordial ova, from $\frac{1}{1650}$ to $\frac{1}{1000}$ of an inch. In the adult, the smallest follicles measure from about $\frac{1}{800}$ to $\frac{1}{600}$ of an inch, and the smallest ova, a little more than $\frac{1}{1000}$ of an inch. The primordial ova have the form of rounded cells, each with a large, clear nucleus, and a nucleolus. Other structures are developed in and surrounding these cells, as they arrive at their full development.

The most interesting stage in the development of the ova and Graafian follicles is observed at about the period of puberty. At this time, a number of follicles (twelve, twenty, thirty, or even more) enlarge, so that we have all sizes, between the smallest primordial follicles, $\frac{1}{800}$ of an inch, and the largest, nearly $\frac{1}{2}$ an inch in diameter. In follicles that have attained any considerable size, we have the fully-developed ova, one in each follicle, except in very rare instances, when there are two, and these ova have a pretty uniform diameter of about $\frac{1}{125}$ of an inch. In the process which culminates in the discharge of the ovum into the fimbriated extremity of the Fallopian tube, the Graafian follicle gradually enlarges, becomes distended with liquid, and finally breaks through and ruptures upon the surface of the ovary. It becomes necessary, then, to study the structure of these large follicles and their relations to the ova; but, before we do this, we can review, with advantage, the relations of the different portions of the ovary and the follicles and ova of various sizes, by an examination of Fig. 271.

Fig. 271 shows the follicles and ova of various sizes. It is observed that the larger follicles contain fully-formed ova and have a proper fibrous coat. The ova here present an epithelial covering and are embedded in a mass of the epithelial lining of the follicle (membrana granulosa), this mass being called the discus or cumulus proligerus.

According to the measurements given by Waldeyer, the smallest Graafian follicles are from $\frac{1}{800}$ to $\frac{1}{600}$ of an inch in diameter, while the largest measure from $\frac{2}{5}$ to $\frac{1}{2}$ an inch. At or near the period of their maturity, the follicles present several coats and are filled with an albuminous liquid. The mature follicles project just beneath the surface and form little, rounded, translucent elevations. The smallest follicles are near the surface, and, as they enlarge, at first become deeper, as is seen in Fig. 271, becoming superficial only as they approach the period of fullest distention.

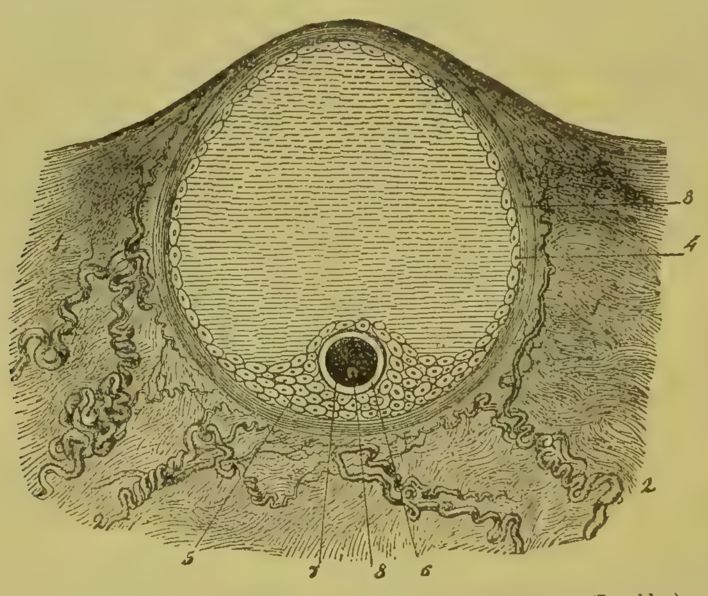


Fig. 272.—*Graafian follicle; magnified 30 diameters.* (Luschka.)
1, 1, stroma of the ovary; 2, 2, convoluted, cork-screw blood-vessels; 3, fibrous wall of the follicle; 4. membrana granulosa; 5, cumulus proligerus; 6, zona pellucida of the ovum; 7, vitellus of the ovum; 8, germinal vesicle with the germinal spot.

Taking one of the largest follicles as an example, two fibrous layers can be distinguished; an outer layer, of ordinary connective tissue, and an inner layer, the tunica propria, formed of the same kind of tissue, with the difference that, as the follicle enlarges, the inner layer becomes vascular. The vascular tunica propria is lined by cells of epithelium, forming the so-called membrana granulosa. At a certain point in this membrane, is a mass of cells, called the discus or cumulus proligerus, in which the ovum is embedded. The situation of the discus proligerus and the ovum has been a subject of discussion. Some anatomists describe it in the most superficial portion, and others, in the deepest part of the follicle. Waldeyer states that he has observed it in both situations; and it is probable that its position is not invariable.

The liquid of the Graafian follicle is alkaline, slightly yellowish, not viscid, and it contains a small quantity of albuminoid matter coagulable by heat, alcohol, and acids. This liquid is supposed to be secreted by the cells lining the inner membrane of the follicle.

It is important to remember that the ovum is not a product of secretion, nor can the ovary be properly considered as a glandular organ. The ovum is an anatomical element; and the ovary is the only organ in which this anatomical element can be developed. The only process of secretion which takes place in the ovary is the production, probably by the cells of the membrana granulosa, of the liquid of the Graafian follicles.

The Parovarium.—The parovarium, or organ of Rosenmüller, is simply the remains of the Wolffian body, lying in the folds of the broad ligament, between the ovary and the Fallopian tube. It consists of from twelve to fifteen tubes of fibrous tissue, lined by ciliated epithelium, and it has no physiological importance. The Wolffian bodies will be fully described in connection with the development of the genito-urinary system.

The Uterus.—The form, situation, and relations of the uterus and Fallopian tubes have already been indicated and are shown in Fig. 270.

The uterus is a pear-shaped body, somewhat flattened antero-posteriorly, presenting a fundus, a body, and a neck. At its lower extremity, is an opening into the vagina,

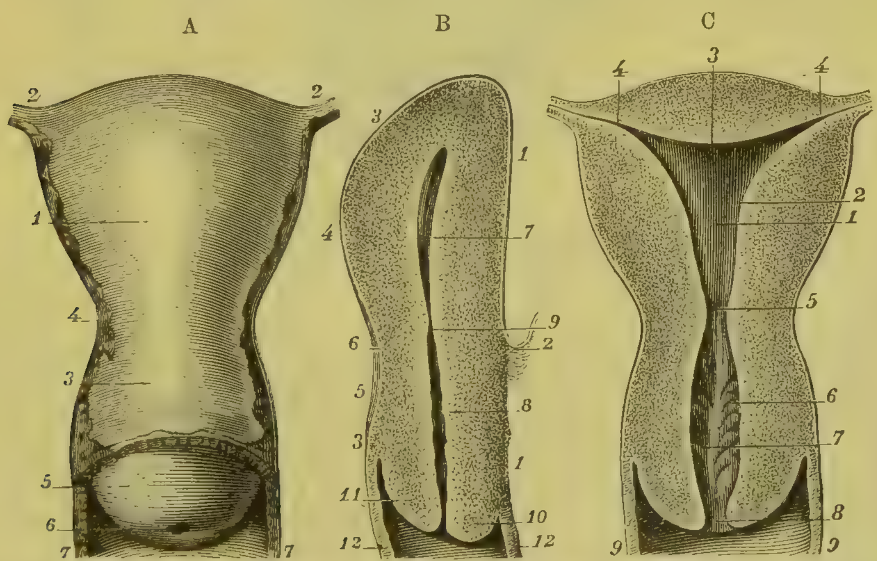


FIG. 273.—*Virgin uterus.* A.—*anterior view.* B.—*median section.* C.—*transverse section.* (Sappey.)
A. 1, body; 2, 2, angles; 3, cervix; 4, site of the os internum; 5, vaginal portion of the cervix; 6, external os; 7, 7, vagina.
B. 1, 1, profile of the anterior surface; 2, vesico-uterine *cul-de-sac;* 3, 3, profile of the posterior surface; 4, body; 5, neck; 6, isthmus; 7, cavity of the body; 8, cavity of the cervix; 9, os internum; 10, anterior lip of the os externum; 11, posterior lip; 12, 12, vagina.
C. 1, cavity of the body; 2, lateral wall; 3, superior wall; 4, 4, cornua; 5, os internum; 6, cavity of the cervix; 7, arbor vitæ of the cervix; 8, os externum; 9, 9, vagina.

called the os externum. At the upper portion of the neck, is a constriction, which indicates the situation of the os internum. The form of the uterus is shown in Fig. 273 (A). It is usually about three inches in length, two in breadth, at its widest portion, and one inch in thickness. Its weight is from one and a half to two and a half ounces. It is somewhat loosely held in place by the broad and round ligaments and by the folds of the peritoneum in front and behind. The delicate layer of peritoneum which forms its external covering extends behind as far down as the vagina, where it is reflected back upon the rectum, and anteriorly, a little below the upper extremity of the neck (os internum), where it is reflected upon the urinary bladder. At the sides of the uterus, the peritoneal covering, a little below the entrance of the Fallopian tubes, becomes loosely attached and leaves a line for the penetration of the vessels and nerves. Fig. 273 (C), giving a view of the interior

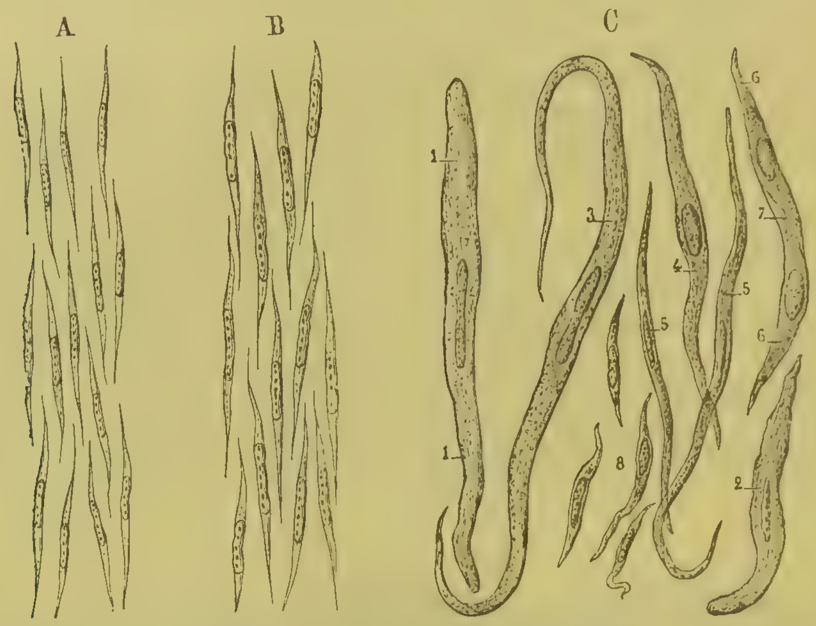


Fig. 274.—*Muscular fibres of the uterus.* (Sappey.)
A, fibres of the uterus of the fœtus at term ; B, of a woman twenty years of age; C, of a woman just delivered.

of the uterus, shows a triangular cavity, with two cornua, corresponding to the openings of the Fallopian tubes, and exceedingly thick walls, the greatest part of which is composed of layers and bands of non-striated muscular fibres.

The muscular walls of the uterus are composed of fibres of the involuntary variety, arranged in several layers. These fibres are spindle-shaped, always nucleated, the nucleus presenting one or two large granules, which have been taken for nucleoli. They are closely bound together, so that they are isolated with great difficulty. In addition to an amorphous adhesive substance between the muscular fibres, we find numerous rounded and spindle-shaped cells of connective tissue of the variety called embryonic, and a few elastic fibres. The muscular tissue of the uterus is remarkable from the fact that the fibres enlarge immensely during gestation, becoming, at that time, ten or fifteen times as long and five or six times as broad as they are in the unimpregnated state. They are united into bundles, or fasciculi, which, in certain of the layers, interlace with each other in every direction.

It is quite difficult to follow out the course of the fasciculi of the muscular tissue of the uterus, and the layers of fibres are described somewhat differently by different writers. All agree, however, that there is a superficial layer, tolerably distinct, very thin, resembling the platysma myoides, which is sometimes called the platysma of the uterus. In addition to this layer, we shall describe two, making, in all, three layers, an external, middle, and internal, although this division is somewhat arbitrary.

The external muscular layer, which is very thin but distinct, is closely attached to the peritoneum. When the uterus is somewhat enlarged after impregnation, we observe oblique and transverse superficial fibres passing over the fundus and the anterior and posterior surfaces to the sides. Here they are prolonged upon the Fallopian tubes, the round ligament, and the ligament of the ovary, and also extend between the layers of the broad ligament. This external layer is so thin that it cannot be very efficient in the expulsive contractions of the uterus; but, from its connections with the Fallopian tubes and the ligaments, it is useful in holding the uterus in place. It does not extend entirely over the sides of the uterus. Rouget, who has given a very elaborate description of the external layer in the human subject and in various classes of animals, has found it prolonged

FIG. 275.—*Superficial muscular fibres of the anterior surface of the uterus.* (Liégeois.)
a, *a*, round ligaments; *b*, *b*, Fallopian tubes; *c*, *c*, *e*, *e*, transverse fibres; *d*, *f*, longitudinal fibres.

into the ligaments and extending to the ovaries and Fallopian tubes. He regards the uterus and its so-called appendages as lying between two thin, muscular sheets, and considers the action of the muscular fibres as very efficient in producing an engorgement of the erectile tissue of the internal organs, by constriction of the veins. Erection, according to this observer, occurs at the period of menstruation, determines the application of the fimbriated extremity of the Fallopian tubes to the surface of the ovary, and assists in the expulsion of the ovum. These points will be more fully considered under the head of ovulation.

The middle muscular layer is the one most efficient in the parturient contractions of the uterus. It is composed of a thick and complicated net-work of fasciculi interlacing with each other in every direction.

The inner muscular layer is arranged in the form of broad rings, which surround the Fallopian tubes, become larger as they extend over the body of the uterus, and meet at the centre of the organ near the neck.

The mucous membrane of the uterus is of a pale, reddish color; and that portion lining the body is smooth, and so closely attached to the subjacent structures, that it cannot be separated to any great extent by dissection. There is, however, no proper submucous areolar tissue, the membrane being applied directly to the uterine walls. It is covered by a single layer of cylindrical epithelial cells with delicate cilia, the movements of which are from without inward, toward the openings of the Fallopian tubes. Examination of the surface of the membrane with a low magnifying power shows the openings of numerous tubular glands. These glands are usually simple, sometimes branched, dividing, about midway between the opening and the lower extremity, into two and, very rarely, into three secondary tubules. Their course is generally tortuous, so that their length frequently exceeds the thickness of the mucous membrane. The openings of these tubes are about $\frac{1}{350}$ of an inch in diameter.

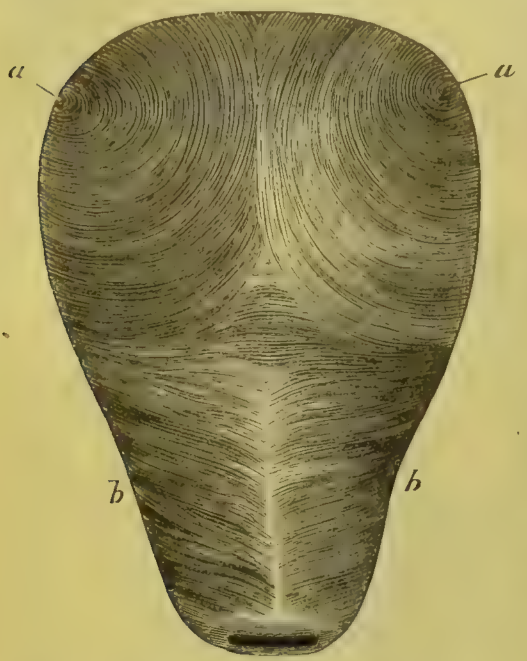


FIG. 276.—*Inner layer of muscular fibres of the uterus.* (Liégeois.)
a, *a*, rings around the openings of the Fallopian tubes; *b*, *b*, circular fibres of the cervix.

The uterine tubes are of considerable physiological interest and have been the subject of much discussion. Their secretion, which forms a thin layer of mucus on the surface of the membrane in health, is grayish, viscid, and feebly alkaline. The tubes themselves have exceedingly thin, structureless walls, and are lined with cylindrical ciliated epithelial cells.

The changes which the mucous membrane of the body of the uterus undergoes during menstruation are remarkable. Under ordinary conditions, its thickness is from $\frac{1}{25}$ to $\frac{1}{14}$ of an inch; but it measures, during the menstrual period, from $\frac{1}{6}$ to $\frac{1}{4}$ of an inch.

In the cervix, the mucous membrane is paler, firmer, and thicker than the membrane of the body of the uterus, and between these two surfaces, there is a distinct line of demarkation. It is here more loosely attached to the subjacent tissue in the cervix, and the anterior and posterior surfaces of the neck present an appearance of folds radiating from the median line, forming what has been called the arbor vitæ uteri, or plicæ palmatæ. These so-called folds are supposed by some anatomists to be formed by rows of large, papillary elevations of the membrane. Throughout the entire cervical membrane, are numerous mucous glands, and, in addition, in the lower portion, are a few rounded, semitransparent, closed follicles, called the ovules of Naboth, which are probably cystic enlargements of obstructed follicles. The upper half of the cervical membrane is smooth, but the lower half presents numerous villi. The epithelium of the cervix presents great variations in its character in different individuals. Before the time of puberty, the entire membrane of the cervix is covered with ciliated epithelium. After puberty, however, the epithelium of the lower portion changes its character, and we have cylindrical cells above, with squamous cells in the inferior portion. The latter extend upward in the neck to a variable distance.

The blood-vessels of the uterus are very large and present certain important peculiarities in their arrangement. The uterine arteries pass between the layers of the broad ligament to the neck, and then ascend by the sides of the uterus, presenting an exceedingly rich plexus of convoluted vessels, anastomosing above with branches from the ovarian arteries, sending branches over the body of the uterus, and finally penetrating the organ, to be distributed mainly in the middle layer of muscular fibres. In their course, these vessels present the convoluted arrangement characteristic of erectile tissue and form a sort of mould of the body of the uterus. Rouget calls this the erectile tissue of the internal generative organs. By placing the pelvis in a bath of warm water and injecting what he calls the spongy bodies of the ovaries and uterus by the ovarian veins, he produced a distention of the vessels and a true erection, the uterus executing a movement analogous to that of the penis during venereal excitement.

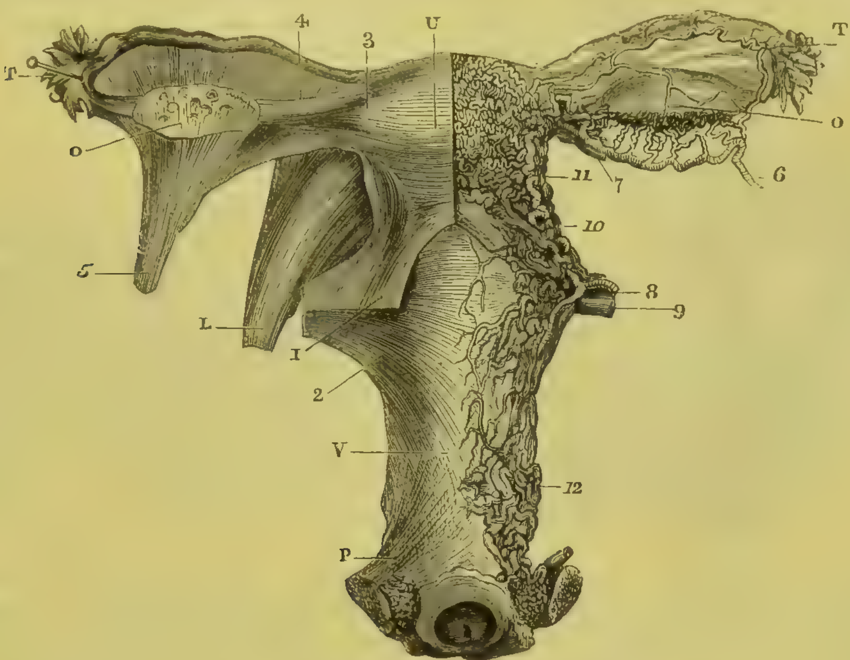


FIG. 277.—*Blood-vessels of the uterus and ovaries; posterior view.* (Rouget.)

T, T, Fallopian tubes; O, O, ovaries; U, uterus; V, vagina; P, pubis; L, anterior round ligament; 1, 2, muscular fibres of the vagina; 3, 4, ligament of the ovary; 5, superior round ligament; 6, ovarian artery; 7, ovarian vein; 8, uterine artery; 9, uterine vein; 10, 11, uterine plexus; 12, vaginal plexus.

In addition to the erectile action above described, Wernich has lately noted a true erection of the lower portion of the uterus, particularly the neck, which he believes to be very efficient in aiding the penetration of spermatozoids. In several observations, he noticed, during a vaginal examination by the touch, that the neck of the uterus, which at first was soft and flaccid, became elongated, hardened, and apparently in a condition of erection, giving an impression to the finger comparable to the hardened glans penis. As an anatomical explanation of the phenomena observed, Wernich quotes from Henle an account of the arrangement of the blood-vessels of the cervix and his physiological deductions from the presence, in this portion of the uterus, of a true erectile tissue. This question will be considered more fully under the head of the mechanism of fecundation.

In the muscular structure of the uterus, are numerous large veins, the walls of which are closely adherent to the uterine tissue. During gestation, these vessels become enlarged, forming the so-called uterine sinuses.

Lymphatics are not very numerous in the unimpregnated uterus, but they become largely developed during gestation. They exist in a superficial and a deep layer, the deeper vessels coming from the muscular substance and probably also from the mucous membrane.

The uterine nerves are derived from the inferior hypogastric and the spermatic plexuses, and the third and fourth sacral. In the substance of the uterus, they present in their course small collections of ganglionic cells and it is said that the nerves pass finally to the nucleoli of the muscular fibres.

The Fallopian Tubes.—The Fallopian tubes, or oviducts, lead from the ovaries to the uterus. They are shown in Fig. 270. These tubes are from three to four inches long, but their length is not always equal upon the two sides. They lie between the folds of the broad ligament at its upper border. Opening into the uterus upon either side at the cornua, they present a small orifice, about $\frac{1}{25}$ of an inch in diameter. From the cornua, they take a somewhat undulatory course outward, gradually increasing in size, so that they are rather trumpet-shaped. Near the ovary, they turn downward and backward. The extremity next the ovary is marked by from ten to fifteen fimbriæ, or fringes, which has given this the name of the fimbriated extremity, or morsus diaboli. All of these

FIG. 278.—*Fallopian tube.* (Liégeois.)

fringe-like processes are free, except one; and this one, which is longer than the others, is attached to the outer angle of the ovary and presents a little gutter, or furrow, extending from the ovary to the opening of the tube. At this extremity, is the abdominal opening of the tube, which is two or three times as large as the uterine opening. Passing from the uterus, the caliber of the tube gradually increases as the tube itself enlarges, and there is an abrupt constriction at the abdominal opening.

Beneath the peritoneal coat, which is formed by the layers of the broad ligament, is a layer of connective tissue, containing a rich plexus of blood-vessels. This constitutes the proper fibrous coat of the Fallopian tubes.

The muscular layer is composed mainly of circular fibres of the non-striated variety, with a few longitudinal fibres prolonged over the tube from the external muscular layer of the uterus. This coat is quite thick and sends bands between the layers of the broad ligament to the ovary, which are supposed to act in adapting the fimbriated extremity of the tube to the surface of the ovary.

The mucous membrane of the tube is thrown into folds, which are longitudinal and transverse near the uterus, and are more complicated at the dilated portion. In this portion, next the ovary, embracing about the outer two-thirds, the folds project far into the caliber of the tube. These are sometimes simple, but more frequently they present secondary folds, often meeting as they project from opposite sides. This arrangement gives an arborescent appearance to the membrane on transverse section of the tube. The mucous membrane is covered by cylindrical ciliated epithelium, the movement of the cilia being from the ovary toward the uterus. At the margins of the fimbriæ, the ciliated epithelium is continuous with the epithelium of the peritoneum, presenting the exceptional example of an opening of a mucous-lined tube into the cavity of the peritoneum. The membrane of the tubes has no mucous glands.

It is not necessary to enter into a minute description of the external organs of the female. Opening by the vulva, externally, and terminating at the neck of the uterus, is a membranous tube, the vagina. This lies between the bladder and the rectum. It has a curved direction, being about four inches long in front, and five or six inches long posteriorly. There is a constricted portion at the outer opening, where we have a muscle, called the sphincter vaginæ, and the tube is somewhat narrowed at its upper end, where it embraces the cervix uteri. The inner surface presents a mucous membrane, marked by transverse rugæ, with papillæ and mucous glands. Its surface is covered with flattened epithelium. The vagina is quite extensible, as it must be during parturition, to allow

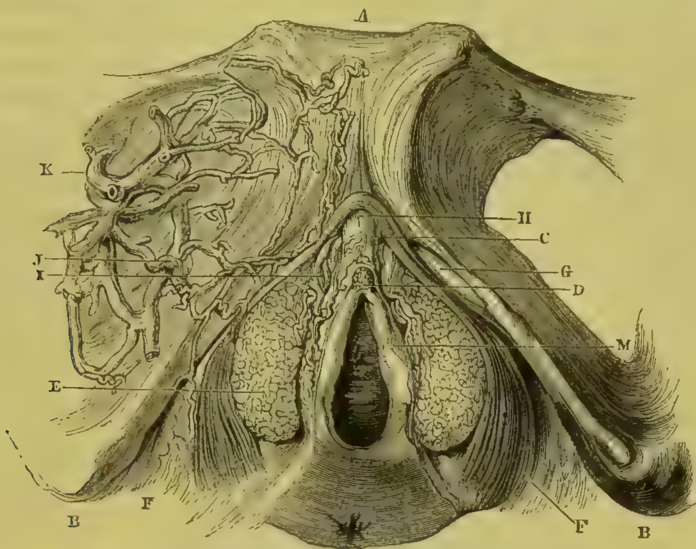


FIG. 279.—*External erectile organs of the female.* (Liégeois.)
A, pubis; B, B, ischium; C, clitoris; D, gland of the clitoris; E, bulb; F, constrictor muscle of the vulva; G, left pillar of the clitoris; H, dorsal vein of the clitoris; I, intermediary plexus; J, vein of communication with the obturator vein; K, obturator vein; M, labia minora.

the passage of the child. It presents a proper coat of dense fibrous tissue, with longitudinal and circular muscular fibres of the non-striated variety. We have, also, surrounding it, a rather loose erectile tissue, which is most prominent at its lower portion.

The parts composing the external organs are abundantly supplied with vessels and nerves. In the clitoris, which corresponds to the penis of the male, and on either side of the vestibule, we find a true erectile tissue.

Structure of the Ovum.

The ripe ovum lies in the Graafian follicle, embedded in the mass of cells which constitutes the discus proligerus. Within the discus, surrounding the ovum, there seem to be two kinds of cells; first, cells evidently belonging to the Graafian follicle and similar to the cells in other parts of the membrana granulosa; second, a single layer of columnar cells belonging to the ovum and probably concerned in the production of the proper membrane of the ovum, the vitelline membrane. Regarding the vitelline membrane as the external covering, we can see, in the ovum, a clear, transparent membrane, a granular mass (the vitellus) filling this membrane completely, a large, clear nucleus, called the germinal vesicle, and a nucleolus, called the germinal spot.

The size of the ripe ovum, in the human subject and in mammals, is about $\frac{1}{125}$ of an inch, and its form is globular.

The external membrane of the ovum is clear, apparently structureless, quite strong and resisting, and it measures about $\frac{1}{2500}$ of an inch in thickness. As it forms a transparent ring in the mass of cells in which the ovum is embedded, this is sometimes called the zona pellucida. According to recent researches, it seems that the primordial ovum has at first no special investing membrane; as it develops, it presents, surrounding the vitellus, a single layer of columnar cells; at the deepest portion of these cells, a homogeneous basement-membrane is gradually formed; and the cells undergo a sort of cuticular transformation, becoming finally the vitelline membrane.

An important point, in this connection, is the question of the existence of pores, or perforations in the vitelline membrane. As we shall see farther on, there can be no doubt with regard to the actual penetration of the spermatozoids through this membrane, so that they come in contact with the vitellus; and it is in this way that the ovum is fecundated. In the osseous fishes and in mollusks, there seems to be no question with regard to the existence of numerous pores in the vitelline membrane; but these are not so easily demonstrated in the ova of mammals. Admitting the existence of a micropyle and pores in the vitelline membrane in fishes and mollusks, it is certain that openings are very much more indistinct, if they can be seen at all, in the ova of mammals; still, the fact of the actual penetration of spermatozoids almost of necessity presupposes the presence of orifices. We have often thought, in studying this subject, that it must be difficult, examining a perfectly transparent and homogeneous membrane in water, which would fill up all pores, to distinguish any openings, and we have been disposed to admit their presence, mainly because the spermatozoids are known to pass through. The idea of their existence in mammals certainly receives support from analogy with the lower orders of animals.

The vitellus, called the principal yolk or the formative yolk, contains the elements which are to undergo development into the embryon. It is composed of a semifluid mass, containing, in addition to the germinal vesicle, numerous granules. Some of these granules are large, strongly-refracting, globular bodies, which are so bright and so numerous, that they obscure the other parts of the vitellus. Between these, are numerous albuminoid granules, which are much smaller and not so distinct.

The germinal vesicle, sometimes called the vesicle of Purkinje, is the enlarged nucleus of the primordial ovum. It is a clear, globular vesicle, about $\frac{1}{550}$ of an inch in diameter, embedded in the vitellus, its position varying in different ova. It presents in its interior a number of fine granules, and a large, dark spot, called the germinal spot, or the spot of Wagner, which measures about $\frac{1}{3600}$ of an inch in diameter. This spot corresponds to the nucleolus of the primordial ovum. In mammals, the mature ovum contains but one germinal vesicle and one germinal spot. The various points we have described are illustrated in Fig. 280.

Discharge of the Ovum.

A ripe Graafian follicle measures from $\frac{2}{5}$ to $\frac{1}{2}$ of an inch in diameter and presents a rounded elevation, containing a plexus of blood-vessels, upon the surface of the ovary. At its most prominent portion, is an ovoid spot, in which the membranes are entirely free from blood-vessels. At this spot, which is called the macula folliculi, the coverings finally give way, and the contents of the follicle are discharged. For a short time anterior to the rupture of the follicle, important changes have been going on in its structure. In the first place, the non-vascular portion, situated at the very surface of the ovary, undergoes fatty degeneration, by which this part of the wall becomes gradually weakened. At the same time, at the other portions of the follicle, there is a growth of cells, which project into the interior, and an extension, into the interior, of blood-vessels in the form of loops. These changes, with an increase in the pressure of liquid and the fatty degeneration of the macula, cause the follicle to burst; and, with the liquid, the discus proligerus and the ovum are expelled. The formation of a cell-growth in the interior of the follicle is really the beginning of the corpus luteum; and this occurs some time before the discharge of the ovum takes place. It is a disputed question whether or not a hæmorrhage occurs into the follicle at the time of its rupture. This may, and undoubtedly does sometimes occur, but it cannot be regarded as constant and has been denied by many observers.

The time at which the follicle ruptures, particularly with reference to the menstrual period, is probably not definite; but it is certain that, while sexual excitement may hasten the discharge of an ovum by producing a greater or less tendency to congestion of the internal organs, ovulation takes place independently of the action of coition. The opportunities for determining this fact in the human female are not frequent; but it has been fully demonstrated by observations upon the inferior animals, and there is now no doubt with regard to the identity of the phenomena of rut and of menstruation. It is useless, at the present day, to enter into an elaborate discussion of this point, which occupied so much the attention of the earlier writers. From the earliest times, it was recognized, not only that women became fruitful only after the appearance of the menses, but that sexual intercourse was most likely to be followed by conception when it occurred near the periods; a point which we shall discuss more fully under the head of fecundation. When it was recognized that rupture of Graafian follicles was followed by the formation of corpora lutea, it became easy to verify the supposition that the ova were discharged at regular intervals, by an examination of the ovaries in women who had died suddenly; and such observations, showing corpora lutea in virgins, demonstrated that ovulation was not necessarily dependent upon coitus.

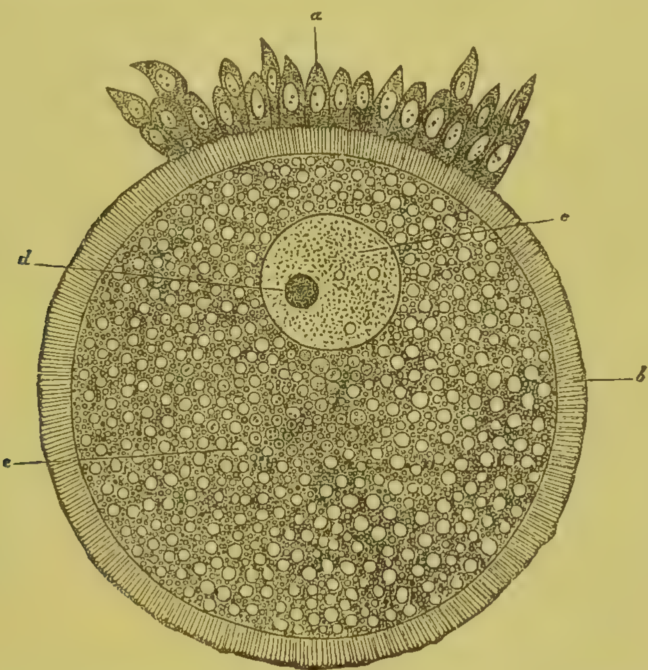


FIG. 280.—*Ovum of the rabbit, from a Graafian follicle* $\frac{1}{20}$ *of an inch in diameter.* (Waldeyer.) *a*, epithelium of the ovum; *b*, zona pellucida, with radiating striations (vitelline membrane); *c*, germinal vesicle; *d*, germinal spot; *e*, vitellus.

Observations upon the lower animals have shown, notwithstanding the fact of discharge of ova without copulation or even the sight of the male, that sexual excitement has a certain influence upon ovulation. The experiments of Coste upon this point are very interesting. This observer noted that, in rabbits killed from ten to fifteen hours after copulation, there was evidence of the recent discharge of ova. In two experiments, however, he took female rabbits in heat and manifesting the greatest ardor for the male, presented them to the male, in order to show that they were really in heat, but carefully prevented copulation. This was done for three days in succession, there being, on each occasion, a manifest desire for the approach of the male. One rabbit was killed on the third day, while still in heat; and six distended Graafian follicles were found in one ovary and two in the other; but there was no trace of ruptured follicles. The other rabbit ceased to be in heat on the fourth day and was killed on the fifth. This animal presented seven distended follicles on one side, and one on the other, but no ruptured follicles. From these and other experiments upon the lower animals, there seems to be no doubt that copulation hastens the rupture of ripe Graafian follicles; but, on the other hand, it is equally true that follicles rupture independently of the sexual act.

To return to the phenomena which attend ovulation in the human subject, there is every reason to suppose, at least from analogy, that the excitement of the genital organs during sexual intercourse may determine the rupture of a ripe Graafian follicle. At stated periods, marked by the phenomena of menstruation, one, and sometimes more Graafian follicles become distended and usually rupture and discharge their contents into the Fallopian tubes. This discharge of an ovum or ova may occur at the beginning, at the end, or at any time during the continuance of the menstrual flow. Upon this point, the observations of Coste, which were made many years ago, seem entirely conclusive. In a woman who died on the first day of menstruation, he found a recently-ruptured follicle; in other instances, at a more advanced period and toward the decline of the menstrual flow, he found evidences that the rupture had occurred later; in the case of a female who drowned herself four or five days after the cessation of the menses, a follicle was found in the right ovary, so distended that it was ruptured by very slight pressure; and other instances were observed in which follicles were not ruptured during the menstrual period. The most striking case of this kind was of a young girl, nineteen years of age, who committed suicide fifteen days after the menstrual period. The ovaries were examined with the greatest care. "By the side of the Graafian vesicles largely developed, were found traces of ruptured vesicles; but the corpora lutea were evidently too old to be reasonably referred to the last menstruation; the Graafian vesicle, consequently, had not matured, or at least had been arrested in its development."

In conclusion, remembering that coitus may hasten the rupture of ripe follicles, we quote from Coste the following as representing what we know of the relations between ovulation and menstruation:

"As a summary, then, of all the facts that I have observed, I believe it to be conclusive, that, in the human female, there is always, at each menstrual period, as during the condition of rut in animals, a vesicle of the ovary which has a marked preponderance over the others; that it spontaneously arrives at maturity, and, most generally, is ruptured at some time during this period to give issue to the ovum which it contains; but there are cases, also, in which, in the absence of sufficiently favorable conditions, this distended vesicle cannot accomplish this end, and, as in mammals again, may remain stationary or be entirely reabsorbed."

Passage of Ova into the Fallopian Tubes.

The fact that the ova, in the great majority of instances, pass into the Fallopian tubes, is sufficiently evident. The fact, also, that ova may fall into the cavity of the peritoneum is shown by the occasional occurrence of extra-uterine pregnancy, a rare accident, which shows that, in all probability, the failure of unimpregnated ova to enter the tubes is exceptional. When we come, however, to the mechanism of the passage of the ova into the tubes, the explanation is difficult. At the present time there are two theories with regard to this process; one, in which it is supposed that the fimbriated extremities of the Fallopian tubes, at the time of rupture of the Graafian follicles, become adapted to the surface of the ovaries; and the other, that the ova are carried to the openings of the tubes by ciliary currents. Neither of these theories is capable of actual demonstration; and we can only judge of their probable correctness from anatomical facts. Rouget, an earnest advocate of the first-mentioned theory, has given an exact description of the muscular structures connected with the tubes and ovaries. We have already seen that one of the fimbriæ of the tube is longer than the others and is attached to the outer angle of the ovary. The other fimbriæ are unattached and are distant from about half an inch to an inch from the ovarian surface. According to this observer, there is a double layer of muscular fibres, passing from the lumbar region of the uterus and embracing the whole of the dilated portion of the tube; and the action of these fibres must draw the extremity of the tube toward the ovary and apply it to its surface. That the muscular fibres described by Rouget exist, there can be scarcely a doubt; but that their action is essential to the passage of ova into the Fallopian tubes, is a question for discussion. If we could assume with certainty that the ova are discharged only during sexual intercourse, or that follicles are usually ruptured as a consequence of pressure exerted by the muscular action described by Rouget, this theory would be rendered exceedingly probable, to say the least; but the facts do not admit of this exclusive view. However, observations upon the lower animals, particularly rabbits, have shown that copulation actually hastens the discharge of ova from ripe Graafian follicles; but it must be a question of theory simply, whether the act be attended with the muscular contraction indicated by Rouget, or whether there be a determination of blood to the ovary, which produces an additional tendency to rupture at this time. We can hardly adopt unreservedly the theory of Rouget, unless it be evident that there is no other way in which the ova can enter the tubes. The fact is that, in the human female, an ovum may be discharged at the beginning of menstruation, at any time during the flow, or even after the flow has ceased; and it is more than probable that pressure within the follicle alone may cause its rupture, and that this may occur independently of sexual excitement. In view of these facts, while we cannot deny that the fimbriated extremities of the tubes may, by muscular action, be drawn toward the surface of the ovary, we cannot admit that such an action is constant, or that it is necessary to the passage of ova into the tubes, though the theory of Rouget has been adopted, entirely or in part, by some writers of authority.

If we take into account the situation of the ovaries and the relations of the Fallopian tubes, we can understand how an ovum may pass into the tube, without invoking the aid of muscular action. Let us suppose, for example, that a Graafian follicle be ruptured when the fimbriated extremity of the tube is not applied to the surface of the ovary. One of the fimbriæ, longer than the others, is attached to the outer angle of the ovary and presents a little furrow, or gutter, leading to the opening of the tube. This furrow is lined by ciliated epithelium, as indeed, is the mucous membrane of all of the fimbriæ, the movements of which produce a current in the direction of the opening, which we might suppose would be sufficient to carry a little globule, only $\frac{1}{125}$ of an inch in diameter, into the tube. At the same time, there is probably, as has been suggested by Becker, a constant flow of liquid over the ovarian surface, directed by the ciliary current toward the tube; and when the liquid of the ruptured follicle is discharged, this, with the ovum, takes the same course.

In all probability, what we have just described is the mechanism of the passage of the ova into the Fallopian tubes; and it is possible that the fimbriated extremity may be drawn toward the ovarian surface, though we can hardly understand how it can be closely applied to the ovary and exert any considerable pressure upon the distended follicle. It is proper to note, also, that the conditions dependent upon the currents of liquid directed by the movements of cilia are constant and could influence the passage of an ovum at whatever time it might be discharged, while a muscular action would be more or less intermittent.

It is somewhat difficult to understand the exact mechanism of the passage of an ovum discharged from an ovary into the Fallopian tube upon the opposite side, although it cannot be doubted that this sometimes occurs. Schroeder has collected, from various authors, the reports of several cases, in which an ovum has been discharged, has found its way into the uterus, and has undergone development, one tube being closed and the corpus luteum existing upon the side on which the tube was impervious. In some instances in which the corpus luteum has been found on the side on which the tube was closed, tubal pregnancy has occurred upon the opposite side. In these cases, the ovum must have passed across the uterus. It is possible that, the subject lying upon one side, a current of liquid may have taken a direction from the ovary to the opposite tube, but this can be only a matter of conjecture.

Puberty and Menstruation.

At a certain period of life, usually between the age of thirteen and of fifteen years, the human female undergoes a remarkable change and arrives at what is termed the age of puberty. At this time, there is a marked increase in the general development of the body; the limbs become fuller and more rounded; a growth of hair makes its appearance upon the mons veneris; the mammary glands increase in size and take on a new stage of development; Graafian follicles enlarge, and one or more approach the condition favorable to rupture and the discharge of ova. At this time, also, certain changes are observed in the moral as well as in the physical attributes of the female. There is then a sort of indefinite consciousness of a capacity for new functions, with an indescribable change in feeling for the opposite sex, due to the first development of sexual instincts. The female becomes capable of impregnation, and continues so, in the absence of pathological conditions, until the cessation of the menses.

It is a commonly-recognized fact that the age of puberty is earlier in warm than in cold climates; and numerous instances are on record, in which the menses have appeared exceptionally, much before the usual period. Generally, at the age of forty or forty-five, the menstrual flow becomes irregular, occasionally losing its sanguineous character, and it usually ceases at about the age of fifty years. Sometimes it is said that the menses return, with a second period of fecundity, though this is rare. According to most writers, while climate has a certain influence over the time of cessation as well as the first appearance of the menses, this is not very marked. When the menses appear early in life, they usually cease at a correspondingly early period; but this is by no means constant. There are, also, numerous exceptions to the ordinary limits to the period of fecundity. Haller observed a case of a young girl, nine years of age, who had menstruated for several years, and others, who had become pregnant at nine, ten, and twelve years. He also quotes cases of women who have been fruitful at from fifty-four to seventy years of age. Other instances of this kind are on record, which it is unnecessary to quote. The occurrence of pregnancy after the age of fifty or fifty-five is certainly doubtful.

Menstruation.

It is unnecessary to discuss farther the correspondence between menstruation in the human female and the condition of heat in the lower animals, as we have already seen, under the head of ovulation, that these two conditions are essentially identical. In the lower animals, the female will admit the male only at the period of heat; and, in some animals in the savage state, it is only at this time that the male is capable of copulation. The variations in sexual temperament in the human female are so considerable, and the sentiments toward the opposite sex are so subordinate to artificial conditions of society and civilization, that it is difficult to establish a parallel, in this regard, between her and the lower animals. Some females rarely or never experience sexual excitement and have no orgasm during intercourse; while others seem to be capable of sexual ardor at any time. Women who are in the habit of promiscuous relations with the other sex frequently lose the sexual feeling and simulate excitement during coitus. It is very difficult, indeed, to say positively how far the facts observed in the lower animals are applicable to the human subject, as we must depend largely upon statements which, of themselves, are entitled to but little consideration. It is nevertheless true that, in some women, sexual desire is decidedly marked just after the cessation of the menses, and in many, it really exists at no other time. Still, mercenary or other considerations may induce women to admit intercourse at any time, and the sexual orgasm, and even fecundation, may at any time occur. As a rule, the female yields to advances made by the male and is reputed to experience a less degree of sexual desire and ardor, although this has marked exceptions. It is probably true that, eliminating, as far as we can, all considerations except those of a purely sexual character, there is less of a promiscuous feeling for the opposite sex in females than in males, and that sexual desire, aside from feelings of fatigue or satiety, is sometimes markedly periodical in women. If we may take certain individual cases as representing physiological conditions, it appears that, in some women, there is a period of comparative indifference to the opposite sex; as the menses approach, there is more or less irritability of temper and disinclination for society, which disappear as the flow is established; and, at or following the cessation of the menses, sexual desire is manifested to an unusual degree, this continuing for only a few days.

Although there is a periodical condition of heat in the lower animals, connected with ovulation, a sanguineous discharge from the genital organs is not often observed. It is only in monkeys that we have a counterpart of what occurs in the human female; and observations upon these animals have shown that they are subject to a monthly discharge of blood, at this time giving evidence of unusual salacity.

In the human female, near the time of puberty, there is sometimes a periodical sero-mucous discharge from the genital organs, preceding, for a few months, the regular establishment of the menstrual flow. Sometimes, also, after the first discharge of blood, the female passes several months without another period, when the second flow takes place, and the menses then become regular. In a condition of health, the periods recur every month, until they cease, at what is termed the change of life. In the majority of cases, the flow recurs on the twenty-seventh or the twenty-eighth day; but sometimes the interval is thirty days. As a rule, also, utero-gestation, lactation, and most severe diseases, acute and chronic, suspend the periods; but this has exceptions, as some females menstruate regularly during pregnancy, and it is not very uncommon for the menses to appear during lactation.

As we should naturally expect, from the connection between menstruation and ovulation, removal of the ovaries, especially when this occurs before the age of puberty, is usually followed by arrest of the menses. It is a well-known fact that animals do not present the phenomena of heat after extirpation of the ovaries. Raciborski has quoted cases of this operation in the human subject, in which the menses were arrested; but this rule does not appear to be absolute, as Dr. H. R. Storer reports at least one case, in which menstruation continued with regularity for more than a year after removal of both ovaries. Dr. T. G. Thomas, of New York, in three cases of removal of both ovaries from menstruating women, which he followed for from five and a half months to two years and eleven months after the operation, noted no return of menstruation. In one case, nearly six months after the operation, the patient had "a bloody discharge from the vagina and all the symptoms accompanying the menstrual function." When a cow brings forth twins, one a male and the other apparently a female, the latter is called a free-martin and generally has no ovaries. Hunter, in his paper on the free-martin, gives a full description of this anomalous animal and states that it does not breed or show any inclination for the bull. In 1868, we had an opportunity of examining the generative organs of a free-martin raised and killed by Prof. James R. Wood. In this animal, the uterus was rudimentary and there were no ovaries.

A menstrual period usually presents three stages: first, invasion; second, a sanguineous discharge; third, cessation.

The stage of invasion is variable in different females. There is usually, anterior to the establishment of the flow, more or less of a feeling of general *malaise*, a sense of fulness and weight in the pelvic organs, accompanied with a greater or less increase in the quantity of vaginal mucus, which becomes brownish or rusty in color. It is probable that, at this time, the discharge has a peculiar odor, though this point is somewhat difficult to determine. In the lower animals, at least, there is certainly a characteristic odor during the rutting period, which attracts the male. At this time, also, the breasts become slightly enlarged in the human female, showing the connection between these organs and the organs of generation. This stage may continue for one or two days, although, in many instances, the first evidence of the access of a period is a discharge of blood.

When the general symptoms above indicated occur, the sense of uneasiness is usually relieved by the discharge of blood. During this, the second stage, blood flows from the vagina in variable quantity, and the discharge continues for from three to five days. With regard to the duration of the flow, there are great variations in different individuals. Some women present a flow of blood for only one or two days; while, in others, the flow continues for from five to eight days, within the limits of health. A fair average, perhaps, is four days.[1] It is also difficult to arrive at an approximation, even, of the total quantity of the menstrual flow. Burdach estimated it at from five to six ounces. According to Longet, this estimate is rather low, the quantity ordinarily ranging from ten to twelve ounces, occasionally amounting to seventeen ounces, or even more. It is well known that the quantity is exceedingly variable, as is the duration of the flow, and the difficulties in the way of collecting and estimating the total discharge are evident.

The characters of the menstrual flow are sufficiently simple. Supposing the discharge to continue for four days, on the first day, the quantity is comparatively small; on the second and third, the flow is at its height; and the quantity is diminished on the fourth day. During this, the second stage, the fluid has the appearance of pure arterial blood, not coagulated, and mixed, as has been shown by microscopical examination, with pavement-epithelium from the vagina, cylindrical cells from the uterus, leucocytes, and a certain amount of sero-mucous secretion. Chemical examination of the fluid does not show any marked peculiarities, except that the quantity of fibrin is either not estimated or is given as much less than in ordinary blood.

The mechanism of the hæmorrhage, which will be considered more fully when we come to study the changes in the uterine mucous membrane during menstruation, is probably the same as in epistaxis. There is a rupture of small blood-vessels, probably capillaries, and blood is thus exuded from the entire surface of the membrane lining the uterus, and sometimes from the membrane of the Fallopian tubes. The blood is then discharged into the vagina and is kept fluid by the vaginal mucus. The mucus of the body of the uterus is viscid and alkaline; the mucus secreted at the neck is gelatinous, viscid, tenacious, and also alkaline; the vaginal mucus is decidedly acid, creamy, and not viscid, containing numerous cells of scaly epithelium, and leucocytes.

The third stage, that of cessation of the menses, is very simple. During the latter part of the second stage, the flow of blood gradually diminishes; the discharge becomes rusty, then lighter in color; and, in the course of about twenty-four hours, it assumes the characters observed in the intermenstrual period.

When the menstrual flow has become fully established, there is no very marked general disturbance, except a sense of lassitude, which may become exaggerated if the discharge be unusually abundant. It has been noted, however, by Rabuteau, that, during the menstrual period, the production of urea is diminished more than twenty per cent., that the pulse becomes slower, and that the temperature falls at least one degree (half a degree, centigrade).

[1] Burdach makes the following statement with regard to certain conditions capable of modifying the menstrual flow: "The flow is more abundant in the indolent than in women accustomed to labor; in those of feeble constitution than in those who enjoy robust health; in inhabitants of cities than in inhabitants of villages."

Changes in the Uterine Mucous Membrane during Menstruation.—If the mucous membrane of the uterus be examined during the menstrual flow, it is found smeared with blood, which sometimes extends into the Fallopian tubes. It is then much thicker and softer than during the intermenstrual period. Instead of measuring about $\frac{1}{14}$ of an inch in thickness, as it does under ordinary conditions, its thickness is from $\frac{1}{8}$ to $\frac{1}{4}$ of an inch. It becomes more loosely attached to the subjacent parts, is somewhat rugous, and the glands are very much enlarged. At the same time, there are developed, in the substance of the membrane, numerous spherical and fusiform cells. According to the recent and very striking researches of Kundrat and Engelmann, this condition probably precedes the discharge of blood by several days, during which time, the membrane is gradually preparing for the reception of the ovum. One of the most important points in these researches is that there is a fatty degeneration of the different elements entering into the structure of the mucous membrane, including the blood-vessels, this change being most marked at the surface; and it is on account of the weakened condition of the vascular walls that the hæmorrhage takes place. A short time after the flow has ceased, the mucous membrane returns to its ordinary condition.

We have already noted that there is a considerable desquamation of epithelium from the uterus with the flow of blood, during the menstrual period. Sometimes, in normal menstruation, the epithelium is in the form of patches; and, in certain cases of dysmenorrhea, there is a membranous exfoliation, which has led to the idea that the mucous membrane is actually thrown off. In normal menstruation, there is no true exfoliation of the membrane, and, even in what is called membranous dysmenorrhea, the so-called membrane is usually nothing more than a membraniform exudation, secreted by the mucous surface.

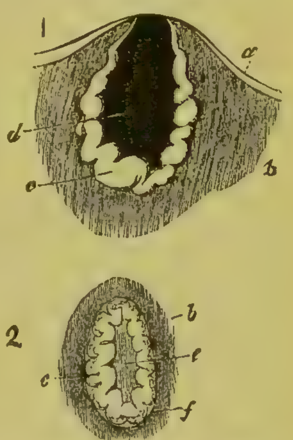


FIG. 281.—*Sections of two corpora lutea; natural size.* (Kölliker.)
1, corpus luteum eight days after conception: *a*, external coat of the ovary; *b*, stroma of the ovary; *c*, convoluted wall of Graafian follicle; *d*, clot of blood.
2, corpus luteum at the fifth month of pregnancy; *b*, stroma of the ovary; *c*, convoluted wall of the Graafian follicle; *e*, decolorized clot; *f*, fibrous envelope of the corpus luteum.

Changes in the Graafian Follicles after their Rupture (Corpus Luteum).—After the discharge of an ovum, its Graafian follicle undergoes certain retrograde changes, involving the formation of what is called the corpus luteum. Even when the discharged ovum has not been fecundated, the corpus luteum persists for several weeks, so that, ovulation occurring every month, several of these bodies, in various stages of retrogression, may sometimes be seen in the ovaries.

For a certain time anterior to the discharge of the ovum, there is a cell-growth from the proper coat of the Graafian follicle, and probably from the membrana granulosa, with a projection of looped blood-vessels into the interior of the follicle, which is the first formation of the corpus luteum. At the time of rupture of the follicle, the ovum, with a great part of the membrana granulosa, is discharged. Sometimes, at the time of rupture of the follicle, there is a discharge of blood into its interior; but this is not constant, though we usually have a gelatinous exudation, more or less colored with blood. At the same time, the follicular wall undergoes hypertrophy, and it becomes convoluted, or folded, and highly vascular. This convoluted wall, formed by the proper coat of the follicle, is surrounded by the fibrous tunic, and its thickening is most marked at the deepest portion of the follicle. At the end of about three weeks, the body—which is now called the corpus luteum, on account of its yellowish or reddish-yellow color—has arrived at the height of its development and measures about half an inch in depth by about three-quarters of an inch in length, its form being ovoid. The convoluted wall then contains a layer of large, pale, finely granular cells, which are internal and are supposed to be the remains of the epithelium of the follicle. The great mass of this wall, however, is composed of large nucleated cells, containing fatty globules and granules of reddish or yellowish pigmentary matter. The thickness of the wall is about one-eighth of an inch, at its deepest portion.

After about the third week, the corpus luteum begins to retract; its central portion and the convoluted wall become paler, and, at the end of seven or eight weeks, a small cicatrix marks the point of rupture of the follicle.

The above are the changes which occur in the Graafian follicles after their rupture and the discharge of ova, when the ova have not been fecundated; and the bodies thus produced are called false corpora lutea, as distinguished from corpora lutea found after conception, which are called true corpora lutea.

Corpus Luteum of Pregnancy.—Before the process of spontaneous ovulation and its connection with menstruation were understood, anatomists were unable to make a definite distinction between the corpus luteum following the discharge of an ovum without fecundation, called the corpus luteum of menstruation, and the corpus luteum of pregnancy. Coste exactly described the various points of distinction between them; and his account of the differences in the development of these bodies, dependent upon the non-fecundation or the fecundation of the ovum, is still regarded as entirely accurate and answers the requirements of science at the present day, even in its medico-legal aspects, as well as in 1847, when his observations were published.

When a discharged ovum has been fecundated, the corpus luteum passes through its various stages of development and retrogression much more slowly than the ordinary corpus luteum of menstruation. It is then called, to distinguish it from the latter, the true corpus luteum. We cannot do better than to quote, in the words of Coste, the description of the changes which this body undergoes in pregnancy:

"I have followed, with the greatest care, in the pregnant female, all the phases of this retrogression. This commences to be really appreciable toward the end of the third month. During the fourth month, the corpus luteum diminishes by nearly a third, and toward the end of the fifth, it is ordinarily reduced one-half. It still forms, however, during the first days after parturition, and in the greatest number of cases, a tubercle which has a diameter of not less than from $\frac{2}{7}$ to $\frac{1}{3}$ of an inch. The tubercle afterward diminishes quite rapidly; but it is nearly a month before it is reduced to the condition of a little, hardened nucleus, which persists more or less as the last vestige of a process so slow in arriving at its final term. Nevertheless, there is nothing absolute in the retrograde progress of this phenomenon. I have seen women, dead at the sixth and even the eighth month of pregnancy, present corpora lutea as voluminous as others at the fourth month.

"Although it may not be, in general, that, after parturition, the corpora lutea disappear, it is nevertheless not without examples that they disappear much more promptly. I have had the opportunity of examining the body of a woman, dead in the course of the eighth month of pregnancy, in whom the absorption was already complete. Facts of this kind are doubtless very rare, as only one has occurred in my observations, notwithstanding the numerous researches to which I have devoted myself for a long time. . . .

"There exists a notable difference between the corpora lutea which are formed as the sequence of conception, and those which occur aside from the conditions developed by impregnation. The duration of the former is much longer than that of the latter, and the volume becomes, also, much more considerable, although their nature is, in truth, identical. I have too often had occasion to remark this, in the ovaries of suicides, to retain the slightest doubt in this regard."

The following table, quoted from Coste, shows the different stages of the corpus luteum of pregnancy. It will be remembered that the corpus luteum of menstruation is at its maximum of development at the end of about three weeks, when it measures half an inch in depth by three-quarters of an inch in length, that it then begins to retract, and becomes a small cicatrix at the end of seven or eight weeks.[1]

Dimensions of the Corpus Luteum at different Stages.

		Corpora lutea.		Observations.
		Long diameter.	Short diameter.	
Stages of pregnancy.	25 to 30 days	$\frac{3}{4}$ inch.	$\frac{1}{2}$ inch.	It is rare that a corpus luteum assumes a spherical form, and that, whatever be the section, its diameters are equal, or nearly so. It generally undergoes, in its development, a sort of compression in the same way as does the ovary. Here, only the long and the short diameters, taken from a section of the copora lutea, have been measured, the ovary being divided longitudinally, and, as it is, generally figured in the plates of the atlas.
	About 40 days	1 "	$\frac{3}{5}$ "	
	2 months	1 "	$\frac{3}{6}$ "	
	3 months	1 "	$\frac{3}{4}$ "	
	In the 4th month	$\frac{3}{5}$ "	$\frac{3}{5}$ "	
	Idem	$\frac{1}{2}$ "	$\frac{2}{5}$ "	
	Idem	$\frac{1}{2}$ "	$\frac{2}{5}$ "	
	In the 5th month	$\frac{3}{5}$ "	$\frac{3}{5}$ "	
	5 months	$\frac{1}{2}$ "	$\frac{1}{2}$ "	
	In the 6th month	$\frac{1}{2}$ "	$\frac{1}{2}$ "	
	7 months	$\frac{2}{5}$ "	$\frac{1}{4}$ "	
	In the 9th month	$\frac{3}{5}$ "	$\frac{2}{5}$ "	
After parturition.	20 hours after	$\frac{2}{5}$ "	$\frac{7}{25}$ "	
	3 days after	$\frac{2}{5}$ "	$\frac{1}{3}$ "	Double gestation.
		$\frac{1}{3}$ "	$\frac{7}{25}$ "	
	Idem	$\frac{2}{5}$ "	$\frac{1}{4}$ "	Double gestation.
		$\frac{2}{5}$ "	$\frac{1}{4}$ "	
	7 days after	$\frac{2}{5}$ "	$\frac{1}{5}$ "	

Male Organs and Elements of Generation.

There is not the same physiological interest attached to the anatomical study of the male genitalia, particularly the external organs, as there is to the corresponding parts in the female, for the reason that the function of the spermatozoids is accomplished within the female organs, where they unite with the ovum and where the processes of development take place. The anatomy of the penis and urethra has a more exclusively surgical interest. As physiologists, we have to study the testicles (organs which correspond to the ovaries, and in which the male generative element is developed), the various glandular structures which secrete fluids forming a part of the ejaculated semen, the mechanism of erection, by which penetration of the male organ into the vagina is rendered possible, the composition of the seminal fluid and the mechanism of its ejaculation, and the course of the semen in the generative passages of the female until it is brought in contact with and fecundates the ovum. As regards the penis, it will be sufficient to describe, as we shall under the head of coitus, the mechanism of erection and of the ejaculation of semen. It will be necessary, however, to study the structure of the testicles and of the various glandular organs connected with the urethra, in order to understand the development of the spermatozoids and the composition of the seminal fluid.

The Testicles.—The testicles are two symmetrical organs, situated, during a certain portion of intra-uterine life, in the abdominal cavity, but finally descending into the scrotum. Within the scrotum, which is a pouch-like process of integument, are the

[1] In 1851, Dr. J. C. Dalton published an essay on the "Corpus Luteum of Menstruation and Pregnancy," in which he pointed out very accurately the different points of distinction between what had been known as the false and the true corpora lutea. These observations it is unnecessary to quote in detail, as the results were almost identical with those obtained by Coste; but they are peculiarly interesting, not only from the accuracy of the descriptions, but as they were made independently, and without any knowledge of the publication by Coste four years before.

two testicles, with their coverings, vessels, nerves, etc. The skin of the scrotum encloses both testicles, but is marked by a median raphe. Immediately beneath the skin, is a loose, reddish, contractile tissue, called the dartos, which forms two distinct sacs, one enveloping each testicle, the inner portion of these sacs fusing in the median line, to form the septum. Within these two sacs, the coverings of each testicle are distinct. These organs are, as it were, suspended in the scrotum by the spermatic cords, the left usually hanging a little lower than the right. The coverings for each testicle, in addition to those just mentioned, are the intercolumnar fascia, the cremaster muscle, the infundibuliform fascia, the tunica vaginalis, and the proper fibrous coat.

The tunica vaginalis is a shut sac of serous membrane, covering the testicle and epididymis, and reflected from the posterior border of the testicle to the wall of the scrotum, lining the cavity occupied by the testicle on either side, and also extending over the spermatic cord. This tunic is really a process of peritoneum, which has become shut off from the general lining of the abdominal cavity. The spermatic cord is composed of the vas deferens, blood-vessels, lymphatics, and nerves, with the various coverings already described, which expand and surround the testicle.

Beneath the tunica vaginalis, are the testicles, with their proper fibrous coat. These organs are ovoid, and flattened laterally and posteriorly. "They are from an inch and a half to two inches long, about an inch and a quarter from the anterior to the posterior border, and nearly an inch from side to side. The weight of each varies from three-quarters of an ounce to an ounce, and the left is often a little the larger of the two." (Quain.) The proper fibrous coat is everywhere covered by the closely adherent tunica vaginalis, except at the posterior border, where the vessels enter and the duct passes out. At the outer edge of this border, is the epididymis, formed of convoluted tubes, presenting a superior enlargement, called the globus major, a long mass running the length of the testicle, called the body, and a smaller enlargement inferiorly, called the globus minor. This, too, is covered with the tunica vaginalis. Between the membrane covering the testicle and epididymis and the layer lining the scrotal cavity, is a small quantity of serum, just enough to moisten the serous surfaces. At the superior portion of the testicle, we usually find one or more small, ovoid bodies, each attached to the testicle by short, constricted processes, which are called the hydatids of Morgagni. These have no physiological importance and are supposed to be the remains of fœtal structures.

The proper fibrous coat of the testicle is called the tunica albuginea. It is white, dense, inelastic, measures about $\frac{1}{25}$ of an inch in thickness, and is simply for the protection of the contained structures. Sections of the testicle, made in various directions, show an imcomplete vertical process of the tunica albuginea, called the corpus Highmorianum, or the mediastinum testis. This is wedge-shaped, about $\frac{1}{6}$ of an inch wide at its superior and thickest portion, is pierced by numerous openings, and lodges blood-vessels and seminiferous tubes. From the mediastinum, numerous delicate, radiating processes of connective tissue pass to the inner surface of the tunica albuginea, dividing the substance of the testicle into imperfect lobules, which lodge the seminiferous tubes. The number of these lobules has been estimated at from one hundred and fifty to two hundred. Their shape is pyramidal, the larger extremities presenting toward the surface, and the pointed extremities situated at the mediastinum.

Lining the tunica albuginea and following the mediastinum and the processes which penetrate the testicle, is a tunic, composed of blood-vessels and delicate connective tissue, called the tunica vasculosa, or pia mater testis.

Lodged in the cavities formed by the trabeculæ of connective tissue, are the seminiferous tubes, in which the male elements of generation are developed. These tubes exist to the number of about eight hundred and forty in each testicle and constitute almost the entire substance of the lobules. The larger lobules contain five or six tubes, the lobules of medium size, three or four, and the smallest frequently enclose but a single tube. Each tube presents a convoluted mass, which can frequently be disentangled under water, particularly if the testicle be macerated for several months in water with a little nitric acid. The entire length of the tube, when thus unravelled, is about thirty inches, and its diameter is from $\frac{1}{200}$ to $\frac{1}{150}$ of an inch. It begins by from two to seven short, blind extremities and sometimes by anastomosing loops. The cæcal diverticula are found usually in the external half of the tube, and their length is from $\frac{1}{12}$ to $\frac{1}{8}$ of an inch. The anastomoses are sometimes between the tubes of different lobules, sometimes between tubes in the same lobule, and sometimes between different points in the same tube. As the tubes pass toward the posterior portion of the testicle, they unite into about twenty straight canals, called the vasa recta, about $\frac{1}{75}$ of an inch in diameter, which penetrate the mediastinum testis. In the mediastinum, the tubes form a close net-work, called the rete testis; and, at the upper portion of the posterior border, they pass out of the testicle, by from twelve to fifteen openings, and are here called the vasa efferentia.

Having passed out of the testicle, the vasa efferentia form a series of small, conical masses, which together constitute the globus major, or head of the epididymis. Each of these tubes, when unravelled, is from six to eight inches long, gradually increasing in diameter, until they all unite into a single, convoluted tube, which forms the body and the globus minor of the epididymis. This single tube of the epididymis, when unravelled, is about twenty feet in length.

The walls of the seminiferous tubes in the testicle itself are composed of connective tissue, a basement-membrane, and a lining of granular, nucleated cells. In the rete testis, it is uncertain whether the tubes have a special fibrous coat or are simple channels in the fibrous structure. They are here lined with pavement-epithelium. In the vasa efferentia and the epididymis, we have a fibrous membrane, with longitudinal and circular fibres of involuntary muscular tissue and a lining of ciliated epithelium. The movement of the cilia is toward the vas deferens. In the lower portion of the epididymis, the cilia are absent. The tubular structures of the testicle, the epididymis, and the commencement of the vas deferens are shown in Fig. 282.

FIG. 282.—*Testicle and epididymis of the human subject.* (Arnold.)
a, testicle; *b*, *b*, *b*, *b*, lobules of the testicle; *c*, *c*, vasa recta; *d*, *d*, rete testis; *e*, *e*, vasa efferentia; *f*, *f*, *f*, cones of the globus major of the epididymis; *g*, *g*, epididymis; *h*, *h*, vas deferens; *i*, vas aberrans; *m*, *m*, branches of the spermatic artery to the testicle and epididymis; *n*, *n*, *n*, ramification of the artery upon the testicle; *o*, deferential artery; *p*, anastomosis of the deferential with the spermatic artery.

At the lower portion of the epididymis, communicating with the canal, there is usually found a small mass, formed of a convoluted tube of variable length, called the vas aberrans of Haller. (*i*, Fig. 282.) This is sometimes wanting, and its function, which cannot be very important, is unknown.

Vas Deferens.—The excretory duct of the testicle extends from the epididymis to the prostatic portion of the urethra and is a continuation of the single tube which forms the body and globus minor of the epididymis. It is somewhat tortuous near its origin and becomes larger at the base of the bladder, just before it is joined by the duct of the seminal vesicle. Near its point of junction with this duct, it becomes narrower. Its entire length is nearly two feet.

The course of the vas deferens is in the spermatic cord to the external abdominal ring, through the inguinal canal to the internal ring, where it leaves the blood-vessels, passes beneath the peritoneum to the side of the bladder, then along the base of the bladder by the inner side of the seminal vesicle, finally joining the duct of the seminal vesicle, the common tube forming the ejaculatory duct, which opens into the prostatic portion of the urethra.

The walls of the vas deferens are thick, abundantly supplied with vessels and nerves, and provided with an external fibrous, a middle muscular, and an internal mucous coat. The greater part of that portion of the tube which is connected with the bladder is dilated and sacculated. The fibrous coat is composed of strong connective tissue. The muscular coat presents three layers; an external, rather thick layer of longitudinal fibres, a thin, middle layer of circular fibres, and a thin, internal layer of longitudinal fibres, all of the non-striated variety. By the action of these fibres, the vessel may be made to undergo energetic peristaltic movements, and this has followed galvanization of that portion of the spinal cord corresponding to the fourth lumbar vertebra, which is described by Budge as the genito-spinal centre.

The mucous membrane of the vas deferens is pale, thrown into longitudinal folds in the greatest part of the canal, and presents numerous additional rugæ in the sacculated portion, these rugæ enclosing little, irregular, polygonal spaces. The membrane is covered with columnar epithelium, which is not ciliated. In the sacculated portion, are numerous mucous glands.

Attached to the vas deferens, near the head of the epididymis, is a little mass of convoluted and sacculated tubes, called the organ of Giraldès, or the corpus innominatum. This body is from $\frac{1}{6}$ to $\frac{1}{4}$ of an inch long and $\frac{1}{12}$ of an inch broad. Its tubes are lined with cells of pavement-epithelium, which are often filled with fatty granules. Generally, the tubes present only blind extremities, but some of them occasionally communicate with the tubes of the epididymis. This organ has no physiological importance. It is regarded by Giraldès as a remnant of the Wolffian body, analogous to the parovarium.

FIG. 283.—*Vas deferens, vesiculæ seminales, and ejaculatory ducts.* (Liégeois.)

a, vas deferens; *b*, seminal vesicle; *c*, ejaculatory duct; *d*, termination of the ejaculatory duct; *e*, opening of the prostatic utricle; *f*, *g*, veru montanum; *h*, *l*, prostate.

Vesiculæ Seminales.—Attached to the base of the bladder and situated externally to the vasa deferentia, are the two vesiculæ seminales. These bodies are each composed of a coiled and sacculated tube, from four to six inches in length when unravelled, and somewhat convoluted, in the natural state, into an ovoid mass which is firmly bound to the vesical wall. The structure of the seminal vesicles is not very unlike that of the sacculated portion of the vasa deferentia. They have an external fibrous coat, a middle coat of muscular fibres, and a mucous lining. Muscular fibres pass over these vesicles from the bladder, both in a longitudinal and in a circular direction, and serve as compressors, by the action of which their contents may be discharged. The mucous coat is pale, finely-reticulated, and is covered with cells of polygonal epithelium, nucleated and containing brownish granules. No mucous glands have been found in its substance.

The vesiculæ seminales undoubtedly serve, in part at least, as receptacles for the seminal fluid, as their contents often present a greater or less number of spermatozoids. Although the mucous membrane of the vesicles seems to produce an independent secretion, the presence of glands has not been demonstrated. The fact that the fluid capable of fecundating the ovum is produced only by the testicles, that the spermatozoids are the true fecundating elements of the male, and that these are developed in the testicles, shows that the spermatozoids found in the seminal vesicles pass into their cavity from the vasa deferentia.

The ejaculatory ducts are formed by the union of the vasa deferentia with the ducts of the vesiculæ seminales on either side and open into the prostatic portion of the urethra. Except that their coats are much thinner, they have essentially the same structure as the vasa deferentia.

Prostate.—Surrounding the inner extremity of the urethra, including what is known as its prostatic portion, is the prostate gland or body. This organ, except as it secretes a fluid which forms a part of the ejaculated semen, has chiefly a surgical interest, so that it is unnecessary to describe minutely its form and relations. It is enveloped in an exceedingly dense, fibrous coat, contains numerous glandular structures opening into the urethra, and presents a great number of non-striated, with a few striated muscular fibres, some just beneath the fibrous coat and others penetrating its substance and surrounding the glands.

The glands of the prostate are most distinct at that portion which lies behind the urethra. In the posterior portion of this canal, are found about twenty openings, which lead to tubes ramifying in the glandular substance. These tubes are formed of a structureless membrane, branching as it penetrates the gland. They present hemispherical diverticula in their course, and terminate in dilated extremities, which are looped and coiled. In the deeper portions of the tubes, the epithelium is columnar or cubical, becoming tesselated near their openings, and sometimes laminated.

The prostatic fluid is probably secreted only at the moment of ejaculation. Its characters will be considered under the head of the seminal fluid; but we may here note that it has been thought by Kraus, that the prostatic fluid has the important function of maintaining the vitality of the spermatozoids. "The spermatozoa, in the absence of the prostatic fluid, cannot live in the mucous membrane of the uterus of mammalia; but with its aid they may live for a long time in the uterine mucus, often more than thirty-six hours."

Glands of the Urethra.—In front of the prostate, opening into the bulbous portion of the urethra, are two small racemose glands, called the glands of Méry or of Cowper. These have each a single excretory duct, are lined throughout with cylindrical epithelium, and secrete a viscid, mucus-like fluid, which forms a part of the ejaculated semen. Sometimes there exists only a single gland, and occasionally, though rarely, both are absent. Their function is probably not very important.

The glands of Littre, found throughout the entire urethra and most abundant on its anterior surface, are simple racemose glands, extending beneath the mucous membrane into the muscular structure, presenting here four or five acini. As these acini are surrounded by muscular fibres, we can readily understand how their secretion may be pressed out during erection of the penis. They are lined throughout with columnar or conoidal epithelium, and secrete a clear and somewhat viscid mucus, which is mixed with the ejaculated semen.

Male Elements of Generation.

The ejaculated seminal fluid contains the male elements of generation; but it must be remembered that the complex fluid known as the semen is composed of anatomical elements developed in the testicle itself, mixed with the secretion of the vasa deferentia, of the vesiculæ seminales, of the glands of the prostate, and of the glands of the urethra. As we shall see when we come to discuss the mechanism of fecundation of the ovum, the spermatozoids are the essential male elements, and these are produced in the substance of the testicle, by a process analogous to that of the development of other true anatomical elements, and not by the mechanism with which we are familiar in secreting glands. The testicles cannot be regarded strictly as glandular organs. They are analogous to the ovaries, and they are the only organs in which spermatozoids can be developed, as the ovaries are the only organs in which the ovum can be formed. If the testicles be absent, the power of fecundation is lost, none of the fluids secreted by the accessory organs of generation being able to perform the functions of the true fecundating elements.

In the healthy male, at the climax of a normal venereal orgasm, from half a drachm to a drachm of seminal fluid is ejaculated with considerable force from the urethra, by an involuntary muscular spasm. This fluid is slightly mucilaginous, grayish or whitish, streaked with lines more or less opaque, and it evidently contains various kinds of mucus. It has a faint and peculiar odor, *sui generis*, which is observed only in the ejaculated fluid and not in any of its constituents examined separately. It is a little heavier than water and does not mix with it or dissolve. After ejaculation, it becomes jelly-like and dries into a peculiar, hard mass, which may be softened by the application of appropriate liquids. The liquid is not coagulated by heat and does not contain albumen. Its reaction is faintly alkaline. It contains, in the human subject, from 100 to 120 parts of solid matter per 1,000.

The chemical constitution of the semen has not been very thoroughly investigated and does not present the same physiological interest as its anatomical characters. Aside from the anatomical elements derived from the testicles and the genital passages, it presents an organic principle (spermatine) which has nearly the same chemical characters as ordinary mucosine. It also contains a considerable quantity of phosphates, particularly the phosphate of magnesia. During desiccation, the characteristic crystals of this salt usually make their appearance; and, in the decomposed fluid, we frequently find crystals of the triple phosphates.

The composite character of the seminal fluid will be better understood if we examine briefly the properties of the different mucous secretions which enter into its composition.

In the dilated portion of the vasa deferentia, the mucous glands secrete a fluid which is the first that is added to the spermatozoids as they come from the testicles. This fluid is brownish or grayish. It contains epithelium, and small, rounded granulations, which are dark and strongly refractive. The liquid itself is very slightly viscid. In the vesiculæ seminales, there is a more abundant secretion of a grayish fluid, with epithelium, little colorless concretions of nitrogenized matter, called by Robin, sympexions, and a few leucocytes. The glandular structures of the prostate produce a creamy secretion, which contains numerous fine granulations. It is chiefly to the admixture of this fluid that the semen owes its whitish appearance. Finally, as the semen is ejaculated, it receives the exceedingly viscid secretion of the glands of Cowper, a certain amount of stringy mucus from the follicles of the urethra, with, perhaps, a little of the urethral epithelium.

Anatomically considered, the seminal fluid contains no important elements except the spermatozoids, the various secretions we have mentioned serving simply as a vehicle for the introduction of these bodies into the generative passages of the female. We shall therefore consider only the structure of the spermatozoids, their movements, and the process of their development.

Spermatozoids.—In August, 1677, a German student, named Von Hammen, discovered the spermatozoids in the human semen, and exhibited them to Leeuwenhoek, who studied them as closely as was possible with the instruments at his command. For a long time, they were regarded as living animalcules; though now they are considered simply as peculiar anatomical elements, endowed with movements, like ciliated epithelium.

These elements are developed within the seminiferous tubes; and they differ, not so much in their mode of development, as in their form, in different animals. We shall describe, however, only the spermatozoids of the human subject.

If we examine a specimen of the fluid taken from the vesiculæ seminales of an adult who has died suddenly, or the ejaculated semen, we find that it contains, in addition to the various accidental or unimportant anatomical elements which we have mentioned, innumerable bodies, resembling animalcules, which present a flattened, conoidal head and a long, tapering, filamentous tail. The caudate appendage is in active motion, and the spermatozoids move about the field of view with considerable rapidity and force, pushing aside little corpuscles or granules with which they come in contact. This is supposed to be an indication of the vitality of the spermatozoids, which are not thought to be capable of fecundating the ovum after their movements have ceased. Under favorable conditions, particularly in the generative passages of the female, the movements continue for days; and this fact is important, as we shall see hereafter, in its bearing upon the limits of the time of fecundation.

FIG. 284.—*Human spermatozoids; magnified 800 diameters.* (Luschka.)

Microscopical examination does not reveal any very distinct structure in the substance of the spermatozoids. The head is about $\frac{1}{5000}$ of an inch long, $\frac{1}{8000}$ of an inch broad, and $\frac{1}{25000}$ of an inch in thickness. The tail is about $\frac{1}{500}$ of an inch in length. La Vallette St. George has found, in man and many of the inferior animals, the "intermediate segment" described first by Schweigger-Seidel, though he does not agree with Schweigger-Seidel that this portion is motionless. The length of the intermediate segment is about $\frac{1}{4000}$ of an inch. It is usually described as the beginning of the tail; and the only difference between this and other portions is that it is a little thicker.

Water speedily arrests the movements of the spermatozoids, which may be restored by the addition of dense saline and other solutions. All of the alkaline animal fluids of moderate viscidity favor the movements, while the action of acid or of very dilute solutions is unfavorable. The movements are suspended by extreme cold, but they return when the ordinary temperature is restored.

Before the age of puberty, the seminiferous tubes are much smaller than in the adult, and they contain small, transparent cells, which, in their form and arrangement, resemble epithelium. As puberty approaches, however, the tubes become larger, and the cell-contents increase in size. At this time, there seem to be two kinds of cells; an epithelium, in the form of irregularly-shaped cells, lining the tubes, and rounded cells, containing one or more nuclei, some of the cells appearing to be in process of segmentation. Many of the cells lining the tubes present a rounded portion, with a large, clear nucleus applied to the tube-wall, each with a caudate prolongation projecting into the tube. Sometimes the projections from the different cells anastomose with each other, forming a kind of network. In the central portions of the tubes of the adult, are rounded vesicles, from $\frac{1}{2250}$ to $\frac{1}{370}$ of an inch in diameter, each containing from two to twenty transparent nuclei measuring from $\frac{1}{5000}$ to $\frac{1}{3000}$ of an inch. In these, which are called the seminal cells, amœboid movements have been observed. The large vesicles with multiple nuclei are the seat of development of the spermatozoids. The nuclei of the vesicles appear to be transformed into the heads of the spermatozoids, and the filamentous appendages, which are seen in the vesicles in various stages of formation, are developed gradually. It often occurs that, when from ten to twenty spermatozoids are developed in a single vesicle, the heads and tails are arranged regularly, side by side; but, when only two or three are observed, their arrangement is irregular. The vesicular envelopes finally disappear and the spermatozoids are liberated; but this occurs only in the rete testis and in the epididymis. In the epididymis and the vasa deferentia, the spermatozoids are motionless, though they are not enclosed in vesicles, apparently from the density of the substance in which they are embedded; for movements are sometimes presented when the contents of the vasa deferentia are examined with the addition of water or saline solutions. Once in the vesiculæ seminales, or after ejaculation, the spermatozoids are invariably in active motion.

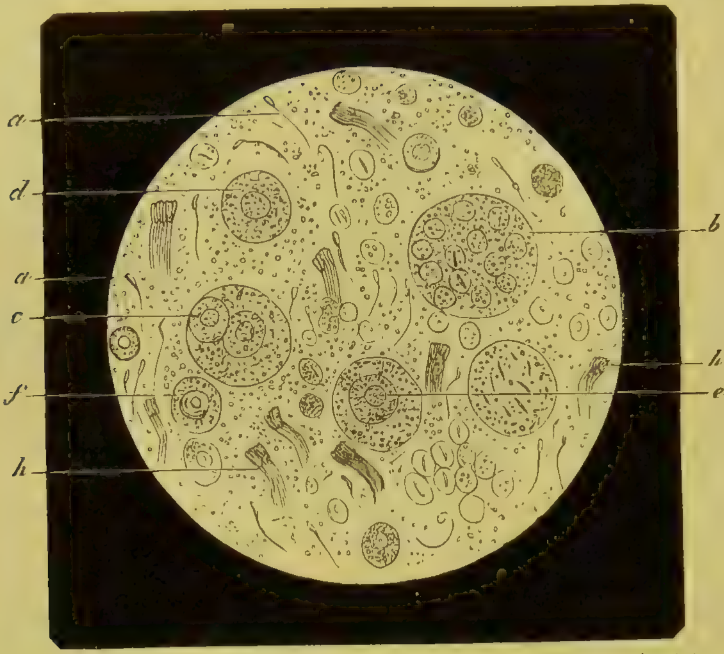


FIG. 285.—*Development of the spermatozoids in the rabbit.* (Liégeois.)

a, *a*, spermatozoids; *b*, spermatic cell containing thirteen nuclei, two of which contain each a head of a spermatozoid developed; *c*, spermatic cell containing two secondary cells, each one provided with a nucleus from which two spermatozoids are to be developed; *d*, *f*, spermatic cells, each with one nucleus; *e*, spermatic cell containing a secondary cell with a nucleus; *h*, bundle of spermatozoids.

The semen, thus developed and mixed with the various secretions before mentioned, is found during adult life and even at an advanced age; and, under physiological conditions, it contains innumerable spermatozoids in active movement. But if sexual intercourse be frequently repeated at short intervals, the ejaculated fluid becomes more and more transparent, homogeneous, and scanty, and it may consist of a small amount of secretion from the vesiculæ seminales and the glands opening into the urethra, without spermatozoids, and consequently deprived of fecundating properties.

In old men, the seminal vesicles may not contain spermatozoids; but this is not always the case, even in very advanced life. Instances are constantly occurring of men who have children in their old age, in which the paternity of the offspring can hardly be doubted. Duplay, in 1852, examined the semen of a number of old men, and found, in about half the number, spermatozoids, normal in appearance and quantity, though, in some, the vesiculæ seminales contained either none or very few. Some of the individuals in whom the spermatozoids were normal were between seventy-three and eighty-two years of age. More recently, M. A. Dieu has investigated the same question. In his conclusions, adding to his own observations the fifty-one cases noted by Duplay, he gives the following results, in one hundred and fifty-six old men:

"25 sexagenarians gave a proportion, still presenting spermatozoids, of 68·5 per 100.

"76 septuagenarians gave a proportion, still presenting spermatozoids, of 59·5 per 100.

"51 octogenarians gave a proportion, still presenting spermatozoids, of 48 per 100.

"4, having passed the age of ninety years, gave entirely negative results."

The oldest man, in the cases reported by Duplay, was eighty-two, and, in those noted by Dieu, eighty-six years, which latter Dieu fixes as the limit, not having observed spermatozoids after that age. The observations were made by examining the contents of the generative passages twenty-four hours after death. Some of the subjects died of acute, and others, of chronic diseases; but the mode of death did not present any differences in the cases classed with reference to the presence of spermatozoids. As a result of his own and other investigations, Dieu comes to the conclusion that the power of fecundation in the male often persists for a considerable time after copulation has become impossible simply from incapacity for erection of the penis.

CHAPTER XXVII.

FECUNDATION AND DEVELOPMENT OF THE OVUM.

Coitus—Action of the male—Action of the female—Entrance of spermatozoids into the uterus—Course of the spermatozoids through the female generative passages—Mechanism of fecundation—Determination of the sex of offspring—Hereditary transmission—Superfecundation—Influence of the maternal mind on offspring—Union of the male with the female element of generation—Passage of the spermatozoids through the vitelline membrane—Deformation and gyration of the vitellus—Polar globule—Vitelline nucleus—Segmentation of the vitellus—Primitive trace of the embryon—Blastodermic layers—Formation of the membranes—Amniotic fluid—Umbilical vesicle—Formation of the allantois and the permanent chorion—Umbilical cord—Membranæ deciduæ—Development and structure of the placenta—General view of the development of the embryon—Development of the cavities and layers of the trunk in the chick—External blastodermic membrane—Intermediate membrane, in two layers—Internal blastodermic membrane—Neural canal—Chorda dorsalis—Primitive aortæ—Vertebræ—Origin of the Wolffian bodies—Pleuro-peritoneal cavity—Development of the skeleton—Development of the muscles—Development of the skin—Development of the nervous system—Development of the encephalon—Development of the organs of special sense—Development of the alimentary system—Formation of the mesentery—Formation of the stomach—Development of the large intestine—Formation of the pharynx and œsophagus—Development of the anus—The liver, pancreas, and spleen—Development of the respiratory system—Development of the face—Development of the teeth—Development of the genito-urinary system—Development of the Wolffian bodies—Ducts of the Wolffian bodies and ducts of Müller—Development of the testicles and ovaries—Development of the urinary apparatus—External organs of generation—Hermaphroditism—Development of the circulatory system—First, or vitelline circulation—Second, or placental circulation—Branchial arches and development of the arterial and the venous system—Development of the heart—Description of the fœtal circulation—Third, or adult circulation.

Coitus.

As far as the male is concerned, coitus is rendered possible by erection of the penis. This may occur before puberty, but, at this time, intercourse cannot be fruitful. As we have seen in a previous chapter, coitus may be impossible in old age, from absence of the power of erection; but spermatozoids may still exist in the vesiculæ seminales, and fecundation might occur, if the seminal fluid could be discharged into the generative passages of the female. Coitus may take place in the female before the age of puberty or after the final cessation of the menses, but intercourse cannot then be fruitful. There are sufficiently numerous examples of conception following what would be called imperfect intercourse, as in cases of unruptured hymen, deformities of the male organs, etc., to show that the actual penetration of the male organ is not essential, and that fecundation may occur, provided the seminal fluid find its way into even the lower part of the vagina. Conception has also followed intercourse, when the female has been insensible or entirely passive; but we shall consider only the physiology of complete and normal intercourse, when both the male and female participate, more or less, in the sexual act.

Action of the Male.—The act of sexual intercourse is preceded, in the male, by a longer or shorter period of excitement, the most important manifestation of which is erection and rigidity of the penis. This is largely controlled by the nervous system. It may be due to distention of the vesiculæ seminales, and, perhaps, of the tubes of the testicle and epididymis after prolonged continence, to the imagination, or to the presence or thought of a female exciting desire. The excitement may, also, be arrested by a sudden feeling of disgust, modesty, or fear; and it sometimes happens that the erethism is so intense that the male organ becomes flaccid without ejaculation. An occurrence of this kind frequently occasions such an amount of mortification and apprehension for the future, that, from the mere dread of a similar accident, there is frequently an incapacity for intercourse when, in all other respects, the conditions are absolutely normal. Physicians have frequent occasion to observe this, especially in the newly-married, who are often afflicted with the fear of permanent sexual incapacity and seek professional advice. This illustrates the influence of the nervous system upon the sexual organs, in the absence of diseased conditions.

Unlike certain of the lower animals, the human subject presents no distinct periodicity in the development of the spermatozoids; but, in reiterated connection, excitement and an orgasm may occur when the ejaculated fluid has no fecundating properties. Such frequently-repeated sexual acts are abnormal; but, from a purely physiological point of view, prolonged continence is equally unnatural and may react unfavorably on the nervous system. No absolute or even approximative rule can be laid down with regard to the frequency with which intercourse may take place within physiological limits. We may assume that these conditions are fulfilled, first, when intercourse is confined within the limits of legitimacy, after the unusual excitement of novelty has passed; second, when both the male and female are in perfect health, and no undue degree of lassitude follows coitus, after a proper period of repose; third, when there is no marked diminution of sexual desire, except that which may be accounted for by age; fourth, when pregnancy occurs at proper intervals, progresses normally, and is followed by the normal period of lactation; fifth, when menstruation is regular, and when there is a period, usually after the cessation of the flow, during which there is unusual sexual excitement, responded to by the male, and disappearing after the sexual desires have been satisfied. It may be somewhat rare to find these conditions fulfilled in all respects, as so few men and women in civilized life are absolutely normal during adult age, and as the sources of unnatural sexual excitement are so numerous; but they approximatively represent the physiological performance of the generative functions in both sexes. It is true that the female can frequently endure sexual excesses better than the male, because she is more passive, and may often not participate in the venereal excitement; but, if we assume that intercourse is physiologically confined within the limits fixed by social laws, the same rules as regards frequency of the sexual act should apply to both. It is certain that intercourse is not normal in the female during menstruation or during the greater part of the period of utero-gestation; and, at these times, it is physiological that the male should be continent. Taking our view chiefly from what appear to be the sexual requirements of the female, intercourse most properly takes place at the time following the menstrual flow, when there is usually a certain amount of sexual excitement, and this should not be immediately repeated, though it may be physiological after a few days. As sexual excitement is gratified and diminishes, intercourse, as far as the desires of the female are concerned, is suspended, and it does not take place to any great extent during pregnancy. This seems to correspond with the normal progress of the generative functions, as we have traced it in the female. It is evident that this is a subject of great delicacy and one that is with difficulty brought to the requirements of rigid scientific inquiry; still it can hardly be avoided in a full account of the physiology of generation, and it is a question often presented to the practical physician.

Although we have not yet considered fully the mechanism of erection, but little remains to be said upon this subject after our discussion, in connection with the circulatory system, of the general structure of erectile tissues. The cavernous and spongy bodies of the penis are usually taken as the type of erectile organs. In these parts, the arteries are large, contorted, provided with unusually thick muscular coats, and connected with the veins by vessels considerably larger than the true capillaries. They are supported by a strong fibrous net-work of trabeculæ which contains non-striated muscular fibres; so that, when the blood-vessels are completely filled, the organ becomes enlarged and hardened and can penetrate the vagina. Researches upon the nerves of erection show conclusively that the vessels of erectile tissues are distended by an enlargement of the arterioles of supply, and that there is not simply a stasis of blood produced by constriction of the veins, except, perhaps, for a short time, during the period of most intense venereal excitement. In experiments upon dogs, Eckhard discovered a nerve derived from the sacral plexus, stimulation of which produced an increase in the flow of blood through the penis, attended with all the phenomena of erection. This nerve arises by two roots at the sacral plexus, from the first to the third sacral nerves. In the experiments referred to, by a comparison of the quantity of venous blood coming from the penis before and during the stimulation of the nerve, Eckhard found a great increase during erection. It is probable that, in addition to the arterial dilatation, when the penis attains its maximum of rigidity, there is a certain amount of obstruction to the outflow of blood, by compression of the veins, and that the rigidity is increased by contraction of the trabecular muscular fibres of the corpora cavernosa.

During erection, the penis becomes exquisitely sensitive, especially at the glans; and the introduction of the organ into the vagina, pressure by the constrictor muscle, and friction, increase this sensibility, until the venereal orgasm occurs. At this time, there is a peculiar and indefinable sensation, almost immediately followed by spasmodic contractions of the vesiculæ seminales and the ejaculatory muscles, and, at the climax of the orgasm, the semen is forcibly discharged from the urethra. This is followed by a feeling of lassitude, a general sense of fatigue of the generative organs, flaccidity of the penis, and it is some time before the venereal appetite can be again excited. Although this is the physiological mechanism of a seminal discharge, friction of the parts is not absolutely necessary, as is shown by the occurrence of orgasm during sleep, which is liable to take place in healthy men after prolonged continence.

After the seminal fluid has been ejaculated during intercourse, the generative act, as far as the male is concerned, is accomplished. It now remains for us to study the action of the female and the process by which the spermatozoids are brought in contact with the ovum.

Action of the Female.—If we can credit the statements made to physicians in their professional intercourse—and we have few other reliable sources of information—there are some females, in whom the generative function is performed, even to the extent of bearing children, who have no actual knowledge of a true venereal orgasm; but there are others who experience an orgasm fully as intense as that which accompanies ejaculation in the male. There is, therefore, the important difference in the sexes, that preliminary excitement and an orgasm are necessary to the performance of the generative act in the male, but are not essential in the female. Still, there can be scarcely a doubt but that venereal excitement in the female facilitates conception, other conditions being favorable.

The first intercourse in the female is usually more or less painful, on account of rupture of the hymen, and the external organs are unduly sensitive until the parts are healed. After this, if there be a preliminary excitement, there is a certain amount of erection of the clitoris (which corresponds to the penis) and of the erectile bulbs situated at the vaginal orifice. There is also an increase in the secretions about these parts, and there may be an ejaculation from two glands opening near the labia minora, called the glands of Bartholinus, which correspond to the glands of Cowper in the male. How far the internal erectile parts participate at this time, it is difficult to determine. By the friction against the clitoris—which, at its maximum of erection, is directed toward the axis of the vagina—against the vaginal walls, and probably, also, by the contact of the glans penis with the neck of the uterus, the excitement of the female increases, the vessels of the vagina become turgid, the secretion of mucus by the external organs becomes abundant, and this finally culminates in an orgasm, similar to that experienced by the male, with a farther increase in the secretion of the glands at the vaginal orifice. As we have stated in our account of the discharge of the ovum from the Graafian follicle, this congestion and excitement may hasten the rupture of a ripe follicle in the human female, as it undoubtedly does in many of the lower animals; but follicles certainly rupture independently of coitus. There is a certain degree of lassitude in the female following sexual intercourse, but this is usually not so marked or so prolonged as in the male.

The most important physiological point in this connection is with regard to the probable action of the internal organs of the female during sexual excitement. We have already studied what has been described as the erectile tissue of the uterus and ovaries. Whether this be or be not a true erectile tissue, seems to be rather a question of definition. The blood-vessels certainly have an erectile arrangement; still, they are not enclosed by those distinct, fibrous trabeculæ which are observed in the penis. In the body of the uterus and in the ovaries, the idea of erection during sexual excitement rests simply upon anatomical descriptions and artificial distention of the vessels after death, and the parts cannot be investigated during life; but it is different with the neck of the uterus, as we shall see farther on; and, upon this point, we may refer to a very remarkable paper, by Dr. Joseph R. Beck, of Fort Wayne, Indiana, which has hardly received, in this country, the attention it deserves. Dr. Beck's observations relate to the question, "How do the spermatozoa enter the uterus?" and, when we consider that it has been positively demonstrated that spermatozoids find their way to the surface of the ovaries, we can appreciate the importance of any reliable observations with regard to the action of the internal organs during coitus.

August 11, 1872, Dr. Beck was called to see a lady, thirty-two years of age, of nervous temperament, blonde, married eight years, with one child, a son, living and seven years old. She had an abortion six years before, and has suffered from symptoms indicating uterine disease ever since. She commenced to menstruate at the age of fourteen. Examination with the finger showed that the os uteri was just inside the vulva, and McIntosh's stem-pessary was introduced. The rest of the history, as the observation is so remarkable, we quote in full:

"Calling at the residence of the patient next day, for the purpose of adjusting the uterine supporter, I made an examination by the touch, and upon introducing my finger between the pubic arch and the anterior lip of the prolapsed cervix, I was requested by her to be very careful in manipulating those parts, as she was very prone, by reason of her passionate nature, to have the sexual orgasm produced by a very slight contact of the finger. Indeed, she stated that this had more than once occurred to her, when making digital investigation of herself. Here then was an opportunity never before offered any one to my knowledge, and one not to be lost on any consideration. Carefully separating the vulvæ with my left hand, so that the os uteri was brought clearly into view in a strong light, I swept the right forefinger across the cervix twice or three times, when almost immediately the orgasm occurred, and the following is what was presented to my view:

"The os and cervix uteri had been firm, hard, and generally in a normal condition, with the os closed so as not to admit the uterine probe without difficulty; but immediately the os opened to the extent of fully an inch, made five or six successive gasps, drawing the external os into the cervix each time powerfully, and at the same time becoming quite soft to the touch. All these phenomena occurred within the space of twelve seconds time certainly, and in an instant all was as before; the os had closed, the cervix hardened, and the relation of the parts had become as before the orgasm.

"Now I carefully questioned my patient as to the nature of the sensations experienced by her at the period of excitement, and she was positive that they were the same in *quality* as they ever were during coition, even before the occurrence of the prolapse; but admits that they were not exactly the same in *quantity*, believing that during coition the orgasm had *lasted longer*, although not at all or in any respect different as to sensation. I had almost forgotten to make mention of the intense congestion of the parts during the 'crisis,' and introduce the statement here."

Certainly, the description we have just quoted is sufficiently graphic, and the mechanism of the penetration of spermatozoids into the uterus, if this be the action of the cervix during an orgasm, seems simple enough; but it cannot explain fecundation, when it occurs, as it undoubtedly may, without orgasm. In physiological literature, we find numerous allusions to a suction force exerted by the uterus during coitus, but this is most frequently stated as of possible or probable occurrence, without being sustained by any positive observations. Still, as early as 1846, we find a direct observation, recorded by Litzmann, as follows:

"I myself lately had the opportunity, in an internal exploration of a young and very erethistic female, of observing that suddenly the uterus assumed a more perpendicular position, was drawn more deeply into the pelvis, the lips of the os uteri immediately became separated, the os became rounded, softer and accessible to the finger, and immediately the highest sexual excitement was betrayed by the respiration and voice."

In considering the mechanism of the penetration of spermatozoids into the uterus, it is also necessary to take into account the secretions, particularly of the mucous glands at the neck. Most writers of the present day admit that, during the height of the orgasm, there is an ejaculation from the uterus of a small amount of alkaline mucus. That an erection of the cervix, followed by sudden relaxation and opening of the os, may occur, cannot be doubted, and there is no evidence of a muscular action in the uterus sufficient to project this fluid forcibly, as the semen is discharged by the male. Assuming that the views just stated be correct, we can readily understand how the neck may be erected and hardened during the orgasm, extruding an alkaline mucus, that the semen is ejaculated forcibly toward the uterus and becomes mixed with the mucus, and that the sudden relaxation of the cervix and opening of the os may exert a force of aspiration and thus draw in the fecundating elements. Certain it is that spermatozoids may be found in the mucus of the cervix a very short time after coitus. It is possible, also, that a sexual connection may be occasionally even more intimate, and that a portion of the glans penis may be actually embraced by the dilated cervix, though this must be unusual. This latter idea of the establishment of a "continuous canal" during intercourse is one that was advanced by many of the older writers.

Quite a strong argument in favor of the view that the spermatozoids are imprisoned, as it were, in the cervical mucus soon after ejaculation, is the fact that vaginal injections immediately after intercourse, which are frequently resorted to to prevent conception, often fail to produce the desired result, even when they are so thorough as to wash out the vagina completely.

While we must accept as probable the view that the uterus may draw into the neck an alkaline mucus previously ejaculated, and with it a certain amount of seminal fluid, the fact that conception may take place without orgasm on the part of the female, and even without complete penetration of the male organ, shows that the action we have described is not absolutely essential, and that the semen may find its way into the uterus in some other way, which it is certainly very difficult to explain.

Course of the Spermatozoids through the Female Generative Passages.—The spermatozoids, once within the cervix uteri, and in contact with the alkaline mucus, which increases the activity of their movements, may pass through the uterus, into the Fallopian tubes, and even to the surface of the ovaries. Precisely how their passage is effected, it is impossible to say. We can attribute it only to the movements of the spermatozoids themselves, to capillary action, and to a possible peristaltic action of the muscular structures, and must acknowledge that these points have as yet been incapable of positive demonstration.

In a very interesting memoir by Lott, which contains numerous observations bearing upon the mechanism of conception, the experiments upon the behavior of the spermatozoids under the microscope, in the presence of currents observed in the liquid between the two plates of glass, develop some very curious points. It was shown, in these experiments, that motionless spermatozoids followed the currents freely; that, when the current in any part of the field was strong, the moving spermatozoids were carried along with it; but that, when the current was comparatively feeble, spermatozoids endowed with active movements made their way, as it were, against it. In reflecting upon these observations, it has seemed to us that they offered an explanation, to a certain extent, of the passage of spermatozoids in the Fallopian tubes toward the ovaries. It is undoubtedly true that the ciliary motion in the Fallopian tubes, in which the direction is from the ovaries toward the uterus, would produce a feeble current. This current would naturally direct the heads of the spermatozoids toward the interior, provided it were not too powerful, and the movements of progression would therefore be from without inward. A little reflection makes it evident that, with a feeble current in the Fallopian tubes from within outward, the spermatozoids, if the current were not strong enough to carry them with it, could only progress in the opposite direction; but this cannot explain the passage of the spermatozoids through the uterus itself, where, according to the best authorities, the ciliary current is from without inward.

As regards the human female, we cannot give a definite idea of the time required for the passage of the spermatozoids to the ovaries or for the descent of the ovum into the uterus; and it is readily understood how these questions are almost incapable of experimental investigation. We know, however, that spermatozoids reach the ovaries, and they have been seen in motion on their surface seven or eight days after connection.

There are many elements of uncertainty in all investigations as to the usual or the normal situation of fecundation. As the spermatozoids are found in movement in all parts of the generative passages, the question resolves itself into that of the duration of vitality of the ovum after its discharge; and here we must rely exclusively upon observations made on the inferior animals. Coste, who demonstrated beyond a doubt that fecundation occurs in fowls at or very near the ovary, recognized fully the difficulties attending similar experiments upon mammals. He succeeded, however, in two observations upon rabbits, in which copulation took place after the period of heat and some time after the discharge of ova. In both of these, he found ova at the superior extremity of the cornua of the uterus, a position which he had found that the ova reached toward the end of the third day. These ova, which were apparently advanced in decomposition, presented no evidence of fecundation and were enveloped in a dense zone of albumen which they had received from the Fallopian tubes. They were surrounded by spermatozoids in active movement, but none had penetrated the adventitious albuminous covering. From these observations, the conclusion is deduced that fecundation can only take place at the ovary or in the most dilated portion of the Fallopian tubes. When we come to apply these observations to the human subject, we have, in confirmation of them, only the abnormal phenomenon of abdominal pregnancy, which cannot occur unless the ovum have been fecundated at the ovary, afterward falling into the abdominal cavity instead of passing to the uterus. Still, the fact that conception may follow a single intercourse occurring at any time with reference to the menstrual period throws a doubt upon the theory that fecundation takes place only at or near the ovary; and another element of uncertainty is in the fact that we do not know positively that ovulation takes place at any definite time before, during, or after the menstrual period, nor do we know precisely how long the spermatozoids may retain their vitality in the female generative passages.

The question of the duration of vitality of the spermatozoids after their passage into the uterus has an important bearing upon the time when conception is most liable to follow sexual intercourse. The alkaline mucus of the internal organs actually favors their movements; the movements are not arrested by contact with menstrual blood; and, indeed, when the spermatozoids are mixed with the uterine mucus, they simply change their medium, and there is no reason to believe that they may not retain their vitality as well as in the mucus of the vesiculæ seminales. We cannot, therefore, fix any limit to the vitality of these anatomical elements under physiological conditions; and we cannot say positively that spermatozoids may not remain in the Fallopian tubes and around the ovary, when intercourse has taken place immediately after a menstrual period, until the ovulation following. There is an idea, based upon rather general and indefinite observation, that conception is most liable to follow an intercourse which occurs soon after a monthly period; but it is certain that it may occur at any time. It is extremely probable that, during the unusual sexual excitement which the female generally experiences after a period, the action of the internal organs attending and following coitus presents the most favorable conditions for the penetration of the fecundating elements, and this may explain the more frequent occurrence of conception as a consequence of intercourse at this time.

Mechanism of Fecundation.—In considering the intimate mechanism of fecundation, we may begin with the proposition that this is accomplished by an actual union with the substance of the ovum of a greater or less number of spermatozoids. This fact, which has long since been positively demonstrated by experiments, affords a material explanation of hereditary transmission, not only of maternal, but of paternal physical and mental qualities.

There are many questions connected with hereditary transmission, which, if they were susceptible of any thing approaching a positive scientific explanation, would be of great interest and might appropriately be discussed in a work upon physiology; but, although the facts of hereditary influence, as regards the inheritance both of physiological and morbid attributes and tendencies, the influence of the maternal mind upon the development of the fœtus, the effects of previous pregnancies, etc., cannot be doubted, their consideration would involve little more than a mere enumeration of remarkable phenomena.

The first question which naturally arises, and which has engaged the attention of ancient as well as modern authors, relates to the conditions which determine the sex of the offspring. The older writers, whose exact physiological knowledge was comparatively limited, were able to present explanations of some of the phenomena of generation, which were more or less satisfactory in their day; but many of these have been contradicted by more recent facts, which have only rendered the causes of the phenomena more obscure. Iconoclasm in physiology is almost a necessary consequence of the acquisition of definite knowledge; and too often the exact student must fail to substitute any thing to supply the places of the broken images of antiquity. This is illustrated in the question of the determination of the sex of offspring. Statistics show clearly enough the proportions between male and female births; but nothing has ever been done in the way of procreating male or female children at will. According to Longet, the proportion of male to female births is about 104 to 105, these figures presenting certain modifications under varying conditions of climate, season, nutrition, etc. It has been shown, by very extensive observations upon certain of the inferior animals, that the preponderance of sex in births bears a certain degree of relation to the vigor and age of the parents; and that old and feeble females fecundated by young and vigorous males bring forth a greater number of males, and *vice versa;* but no exact laws of this kind have been found applicable to the human subject. The idea that one testicle produces males and the other, females, or that the two ovaries have distinct functions in this regard, has no foundation in fact; for men with one testicle, or females with a single ovary, produce offspring of both sexes.

Two ideas with regard to the determination of sex in the fœtus have obtained at different times. One of these is that the sex is dependent upon nutritive or other conditions subsequent to fecundation, and the other, that the sex is determined at the time of union of the male with the female element. Of these two opinions, the weight of evidence appears to be in favor of the latter. Aside from facts in comparative physiology, it is pretty certain that several spermatozoids are necessary for the fecundation of a single ovum. It may be that, when just enough of the male element unites with the ovum to secure fecundation, or when it might be said that the female element predominates, the fœtus is a female, and when a greater number of spermatozoids unite with the vitellus, the male sex is determined. Such an idea, however, is purely theoretical; and the question of the determination of sex presents thus far hardly the shadow of a satisfactory explanation.

No definite rule can be laid down with regard to the transmission of mental or physical peculiarities to offspring. Sometimes the progeny assumes more the character of the male than of the female parent, and sometimes the reverse is the case, without any reference to the sex of the child; sometimes there appears to be no such relation; and occasionally we note peculiarities derived apparently from grandparents. This is true with regard to pathological as well as physiological peculiarities, as in inherited tendencies to certain diseases, malformations, etc.

A peculiar, and it seems to be, an inexplicable fact is that previous pregnancies have an influence upon offspring. This is well known to breeders of animals. If a pure-blooded mare or bitch have been once covered by an inferior male, in subsequent fecundations the young are apt to partake of the character of the first male, even if they be afterward bred with males of unimpeachable pedigree. What the mechanism of the influence of the first conception is, we can form no definite idea; but the fact is incontestable. The same influence is observed in the human subject. A woman may have, by a second husband, children who resemble a former husband, and this is particularly well marked in certain instances by the color of the hair and eyes. A white woman who has had children by a negro may subsequently bear children to a white man, these children presenting some of the unmistakable peculiarities of the negro race.

Superfecundation of course does not come in the category of influences such as we have just mentioned. It is not infrequent to observe twins, when two males have had access to the female, which are entirely distinct from each other in their physical character; a fact which is readily explained by the assumption that two ova have been separately fecundated. This view is entirely sustained by observation and experiment. Cases illustrating this point are numerous, but we cite one, simply to add to the number of positive observations.

The following very interesting communication was received in January, 1869, from Dr. John H. Janeway, Assistant Surgeon U. S. A., and it illustrates superfecundation in the human subject; or, at least, that was the view taken by the negro father:

"Frances Hunt, a freedwoman, aged thirty-five years, gave birth to twins, February 4, 1867, in New Kent County, Virginia. One of these twins was black, the other was white. Frances is a mulatto. The black child is much darker than she is. Previous to the parturition, she had given birth to seven children, all single births. She was living at the time of her impregnation in the family of a white man as house-servant, sleeping with a black man at night. She insists, however, that she never had carnal intercourse with a white man. She probably does this because the black man turned her out of his house when he saw that one of the children was white."

This history was accompanied by an excellent photograph of the mother and the two children, a copy of which is given in Fig. 286. One of the children has the color and all characteristics of the negro, and the other looks like a white child. "The mother and children were inmates of Howard Grove Hospital near this city (Richmond), where the picture was taken, and I saw them frequently. Both children are now dead. The black one died first, teething, the other was killed by a tobacco-plaster applied to its abdomen, it is supposed by its mother.

FIG. 286.—*Mulatto mother with twins, one white and the other black.* From a photograph.

"The only negro feature in the white child was its nose. There, its resemblance to its mother was perfect. Its hair was long, light, and silky. Complexion brilliant."

We have already referred to the curious fact that, when a cow gives birth to twins, one male and the other female, the female, which is called the free-martin, is sterile and presents an imperfect development of the internal organs of generation. This has led to the idea that possibly the same law may apply to the human subject, in cases of twins, one male and the other female; but numerous observations are recorded in gynæcological works, showing the incorrectness of this view, to which we may add the following: The author of the report on Rinderpest to the New York State Agricultural Society, 1867, stated that his father was one of twins, male and female, and that his father's twin sister had borne several children.

It has long been a question whether impressions made upon the nervous system of the mother can exert an influence upon the fœtus *in utero*. While many authors admit that violent emotions experienced by the mother may affect the nutrition and the general development of the fœtus, some writers of high authority deny that the imagination can have any influence in producing deformities. It must be admitted that many of the remarkable cases recorded in works upon physiology as instances of deformity due to the influence of the maternal mind are not reliable. It is often the case that, when a child is born with a deformity, the mother imagines she can explain it by some impression received during pregnancy, which she only recalls after she knows that the child is deformed. Still, there are cases which cannot be doubted, but which, in the present state of our knowledge of development and the connection between the mother and the fœtus, we cannot attempt to explain.

Union of the Male with the Female Element of Generation.—The first important step in our positive knowledge of the mechanism of fecundation was the discovery of the spermatozoids, in 1677, to which we have already referred; the second was the demonstration, by Spallanzani, in his experiments upon artificial fecundation, that, when the seminal fluid is carefully filtered, the liquid which passes through has no fecundating properties, the male element remaining on the filter; and the third was the demonstration of the presence of spermatozoids within the vitelline membrane, showing that fecundation consists in a direct union of the male with the female element.

As to the mechanism of the penetration of spermatozoids to the vitellus, we can only refer to the micropyle discovered in the ova of fishes and mollusks, which we have already described. In the ova of the Nephelis, a small species of leech, Robin has seen spermatozoids, to the number of several hundreds, penetrate the vitelline membrane, always at one point, continuing their movements upon the surface of the vitellus. "Almost always, when the penetration has ceased, a bundle of spermatozoids are arrested in the micropyle." We had an opportunity of witnessing a demonstration of these phenomena by Prof. Robin, in 1861, in the ova of the Limnæus stagnalis, and actually saw a spermatozoid half-way through the vitelline membrane. According to numerous direct observations, the spermatozoids move actively around the ovum, collect toward a certain point, and there penetrate the vitelline membrane. Coste, and many other observers whom it is unnecessary to quote, have seen the spermatozoids within the vitelline membrane, in the ovum of the rabbit; and, more recently, Weil has seen spermatozoids wedged in the substance of the zona pellucida, has added blood to the specimen under observation, and has restored the movements of the spermatozoids while in this position. He has also seen, in some instances, perfectly-formed spermatozoids in the very substance of the vitellus.

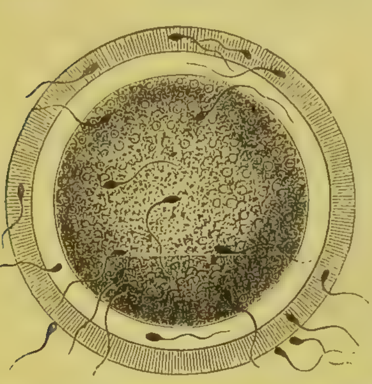


FIG. 287.—*Penetration of spermatozoids through the vitelline membrane.* (Haeckel.)

All direct observations upon the lower orders of animals have shown that several spermatozoids are necessary for the fecundation of a single ovum; but we have no definite idea of the number required in mammals, much less in the human subject. Nor do we know what becomes of the spermatozoids after they have come in contact with the vitellus. All that we can say upon this point is, that there is probably a molecular union between the two generative elements, soon to be followed by the remarkable series of changes involved in the first processes of development.

Segmentation of the Vitellus.

As we have already stated, it is probable that the ovum is fecundated, either just as it enters the Fallopian tube or in the dilated portion near the ovary. As it passes down the tube, whether it be or be not fecundated, it becomes covered with an albuminous layer. This layer probably serves to protect the fecundated ovum, and, when the spermatozoids do not penetrate the vitelline membrane near the ovary, it presents an obstacle to their passage. Shortly after fecundation, the germinal vesicle disappears; but this occurs in ova that have not been fecundated. Soon after ovulation, also, the vitellus gradually withdraws itself from certain portions of the vitelline membrane, or becomes deformed, and then often rotates upon itself; a phenomenon which has long been observed in the ova of some of the lowest orders of animals and of rabbits. The deformation and gyration of the vitellus, however, have been observed in ova before fecundation and have nothing to do with the process of development. They are of the class of movements called amœboid.

After the penetration of spermatozoids and their union with the vitellus, at least in many of the lowest orders of animals, the appearance of the vitellus undergoes a remarkable change, by which ova that are about to pass through the first processes of development may be readily distinguished from those which have not been fecundated. This change consists in an enlargement of the granules and their more complete separation from the clear substance of the vitellus. The granules then refract light more strongly than before, so that the fecundated ova are distinctly brighter than the others. This is the first appearance that is distinctive of fecundation.

Polar Globule.—The next process observed in the ovum is the separation from the vitellus of a comparatively clear, rounded mass, called by Robin the polar globule. This body has been observed before by various anatomists and described under different names. The exact mode of its formation has been studied by Robin in some of the lower

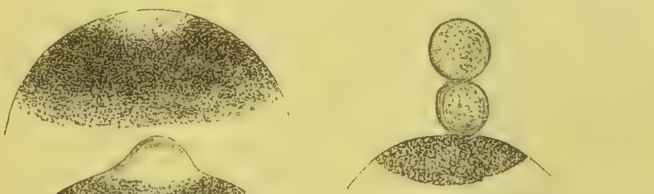


FIG. 288.—*Formation of the polar globules in the ova of the Nephelis octoculata.* (Robin.)

orders of animals. We shall describe briefly this process as it was demonstrated to us by Robin, in 1861, the description being taken from notes made at that time:

Five hours after the entrance of the spermatozoids, we see a little elevation at one point in the vitellus. This is the beginning of the polar globule. It increases in size gradually, and becomes constricted at its base, until it is attached to the vitellus by a

FIG. 289.—*Segmentation of the vitellus.* (Liégeois.)
a, a, a, a, a, spermatozoids. The four upper figures represent the progressive segmentation of the vitellus. The lowest figure shows the cells of the blastoderm.

little pedicle. There is then, usually, a second globule formed just behind the first, in the same manner; and sometimes a third makes its appearance. As soon as the globules are perfectly formed, they all become detached from the vitellus, but remain adherent to each other, gradually fusing to form a single, rounded, very faintly granular mass; and it is opposite this globule that the first furrow of segmentation of the vitellus is observed. The complete formation of the polar globules and their fusion into one occupy three hours. It is probable that the polar globule is formed in the mammalia in the manner above indicated. Sometimes the polar globule is formed in ova that have not been fecundated.

Vitelline Nucleus.—A short time after the complete formation of the polar globule, the germinal vesicle having disappeared, the deformed vitellus resumes its original rounded appearance and fills again the cavity of the vitelline membrane. At this time, the extreme periphery of the vitellus becomes clearer, the granules collect in a large zone around the centre, and, in the centre itself, a clear, rounded body makes its appearance, which is called the nucleus of the vitellus. This mass is viscid, amorphous, without granules, and is entirely different from the germinal vesicle, having no nucleus at first, a nucleolus, however, appearing in each of the numerous nuclei which result from its segmentation. The formation of the nucleus of the vitellus is a positive evidence of fecundation. It appears from fifteen to thirty hours after fecundation.

Segmentation of the Vitellus.—Almost immediately following the phenomena we have just described, the vitellus begins to undergo the remarkable process of segmentation, by which it is divided into numerous small cells. This process may take place to a limited extent in non-fecundated ova; but in this case the cells soon disappear, as the disintegration of the ovum advances. The true segmentation of the vitellus, however, results in the formation of what are called the blastodermic cells. As segmentation has been studied in the inferior animals, there appears first a furrow in the vitellus, at the site of the polar globule, and there is then a furrow on the opposite side, both deepening until the entire vitellus is divided into two globes. These are at first spherical; but they soon become flattened upon each other into two hemispheres. There follows then a similar division into four, another into eight, and so on, until the entire vitellus is divided into numerous cells, each with a clear nucleus resulting from the segmentation of the original nucleus of the vitellus. It is probable that, at first, the cells of the vitellus have no membrane; but a membrane is soon formed, a nucleus appears, and the cells are perfect.

Most of the phenomena of segmentation have been observed in the lower orders of animals; but there can be no doubt that analogous processes take place in the human ovum. In the rabbit, Weil observed, forty-five and a half hours after copulation, an ovum, with sixteen segmentations, situated in the lower third of the Fallopian tube. Ninety-four hours after copulation, he observed an ovum, with a delicate mosaic appearance, presenting a small, rounded eminence on its surface.

It is impossible to say how long the process of segmentation continues in the human ovum. It is stated that it is completed in rabbits in a few days, and, in dogs, that it occupies more than eight days. When the cells of the blastoderm are completely formed, they present a polygonal appearance as they are pressed against the vitelline membrane, their inner surface being rounded. The ovum then contains, within the external layer of cells, a small quantity of liquid. It is probably in this condition that the ovum passes from the Fallopian tube into the uterus, at about the eighth day after fecundation.

Primitive Trace of the Embryon.—The cells formed by the segmentation of the vitellus, after this process is completed, are arranged in the form of a membrane (the blastodermic membrane) which is farther subdivided, as development advances, into layers, which will be fully described hereafter. The albuminous covering which the ovum has received in the upper part of the Fallopian tube gradually liquefies and penetrates the vitelline membrane, furnishing, it is thought, matter for the nourishment and develop-

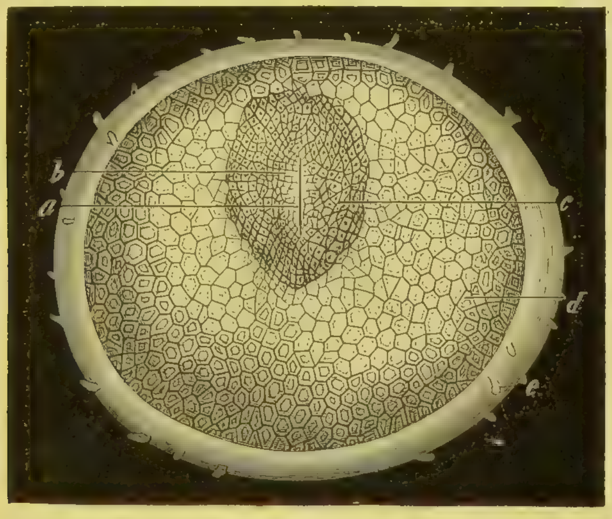


FIG. 290.—*Primitive trace of the embryon.* (Liégeois.)
a, primitive trace; *b*, area pellucida; *c*, area obscura; *d*, blastodermic cells; *e*, villi beginning to appear on the vitelline membrane.

ment of the vitellus. In the Fallopian tube, indeed, the adventitious albuminous covering of the ovum presents an analogy to the albuminous coverings which the eggs of oviparous animals receive in the oviducts; with the difference that this albuminous matter is almost the sole source of nourishment in the latter, and exists in large quantity, while, in viviparous animals, the quantity is small, is generally consumed as the ovum passes into the uterus, and, in the uterus, the ovum forms attachments to and draws its nourishment from the vascular system of the mother.

At the period when the fecundated ovum enters the uterus, it has increased in size about five times. It is then composed of an external covering (the vitelline membrane) with a cellular membrane internal to this (the blastodermic membrane) and a certain amount of liquid in its interior.

Soon after the formation of the single blastodermic membrane, at a certain point on its surface, there appears a rounded elevation or heap of smaller cells, forming a distinct spot, called the embryonic spot. As development advances, this spot becomes elongated and oval. It is then surrounded by a clear, oval area, called the area pellucida, and the area pellucida is itself surrounded by a zone of cells, more granular and darker than the rest of the blastoderm. The elongated line thus formed and surrounded by the area pellucida is called the primitive trace. It has been shown, however, that this primitive trace, or primitive groove, is a temporary structure and has nothing to do with the development of the neural canal. After the groove is formed, there appears in front of, but not continuous with it, a new fold and a groove leading from it. This is the "head-fold," and the groove is the true medullary groove, which is subsequently developed into the neural canal. If we adopt this view—and the difference is not very important—we simply substitute the new trace, which is the seat of the development of the neural canal, for the original primitive trace, which is temporary. It is probable that embryologists have heretofore noted the so-called primitive trace and studied subsequently the development of the true medullary groove, supposing that they were identical structures in different stages of formation, and not observing that the first trace disappears.

Blastodermic Layers.—Shortly after the appearance of the primitive trace, the blastodermic cells, which are at first arranged so as to form a single membrane, separate into layers. These layers have been differently described by various observers, and there is some uncertainty with regard to the application of direct researches made upon the chick, in which most of these early processes of development have been studied, to the mammalia and the human subject. We shall endeavor to describe the different layers in as simple a manner as is consistent with our positive knowledge, omitting all points that are unsettled or which seem to be of minor importance.

The blastodermic cells, resulting originally from the segmentation of the vitellus, are first apparently split into two layers, which may be termed the external and the internal blastodermic membranes. According to the most recent observations, the main portion of the external layer, sometimes called the serous layer, simply forms a temporary investment for the rest of the vitellus and is not developed into any part of the embryon. The internal layer, called the mucous layer, is developed into nothing but the epithelial lining of the alimentary canal. There is a thickening of both of these layers at the line of development of the cerebro-spinal system, with a furrow, which is finally enclosed by an elevation of the ridges and their union posteriorly, forming the canal for the spinal cord.

As the spinal canal is thus developed, a new layer is formed, by a genesis of cells from the internal surface of the original external layer and the opposite surface of the internal, or mucous layer. This layer of new cells may be termed the intermediate layer; and it is from this that nearly all the parts of the embryon are developed.

To summarize the development of the layers just mentioned, we may state that the external layer is a temporary structure; the internal layer is very thin and is for the development of the epithelial lining of the alimentary canal; the most important structure is a thick layer of cells, developed from the opposite surfaces of the external and the internal layer and situated between them, called the intermediate layer; and it is from these cells that the greatest part of the embryon is formed.

Formation of the Membranes.

The brief description we have just given of the formation of the blastodermic layers seemed necessary as an introduction to the study of the membranes; and we shall defer, for the present, the description of their development into the different parts of the embryon.

In the mammalia, a portion of the blastoderm is developed into membranes, by which a communication and union are established between the ovum and the mucous membrane of the uterus. From the ovum, two membranes are developed; one non-vascular, the amnion, and another vascular, the allantois. From the mucous membrane of the uterus, are developed the two layers of the decidua. At a certain part of the uterus, a vascular connection is established between the mucous membrane and the allantois, and the union of these two structures forms the placenta. The fœtal portion of the placenta is connected with the fœtus by the vessels of the umbilical cord; and the maternal portion is connected with the great uterine sinuses. Development takes place from material supplied to the fœtus by the blood of the mother.

The external covering of the ovum, during the first stage of its development, is the vitelline membrane. As the ovum is received into the uterus, the vitelline membrane develops upon its surface little villosities, which are non-vascular and are formed of amorphous matter with granules. These are the first villosities of the ovum, and they assist in fixing the egg in the uterine cavity. They are not permanent, they do not become developed into the vascular villosities of the chorion, and they disappear as the true membranes of the embryon are developed from the blastodermic layers. It is probable that the vitelline membrane disappears about the fourth or fifth day, when it is replaced by the amnion.

Formation of the Amnion.—As the ovum advances in its development, it is observed that a portion of the blastoderm becomes thickened, to form the first trace of the embryon. At this portion, where the body of the embryon subsequently makes its appearance, as we have already seen, we have the external layer, the internal layer, and a thick, intermediate layer of cells, which are developed from the opposite surfaces of the external and the internal layer, called the middle layer. At nearly the time when this thickening begins, a fold of the external layer makes its appearance, surrounding the thickened portion, and most prominent at the cephalic and the caudal extremity of the furrow for the neural canal. This fold increases in extent as development advances, passes over the dorsal surface of the embryon, and finally meets so as to enclose the embryon completely. We can readily figure to ourselves this process and understand how, at a certain period of the development of the amnion, this membrane consists of an external layer, formed of the external layer of the fold, and an internal layer; the point of union of the two layers, or the point of meeting of the fold, being marked by a membranous septum.

The two amniotic layers are formed in the way that we have just described, and a complete separation finally takes place, by a disappearance of the septum formed by the meeting of the folds over the back of the embryon. This process occupies four or five days in the human ovum. The point where the folds meet is called the amniotic umbilicus. When the amnion is thus completely formed, the vitelline membrane has been encroached upon by the external amniotic layer and disappears, leaving this layer of the amnion as the external covering of the ovum. At this time, there is a growth of villosities upon the surface of the external amniotic layer, which, like the villosities of the vitelline membrane, are not vascular.

Soon after the development of the amnion, the allantois is formed. This membrane is vascular, encroaches upon and takes the place of the external amniotic membrane, becomes villous, and its villosities take the place of those of the amnion. Over a certain portion of the membrane, the villosities are permanent. The mode of development of the amnion, as we have described it, is illustrated by the diagrammatic Fig. 291. This figure illustrates the formation of the amnion, the umbilical vesicle, and the allantois. The last two structures are not derived from the external blastodermic layer, and they will be described farther on, after we have studied the full development of the amnion and its relations.

When the allantois has become the chorion, or the external membrane of the ovum, having taken the place of the external layer of the amnion, the structures of the ovum are the following: 1. The chorion, formed of the two layers of the allantois, derived from the internal blastodermic membrane, and penetrated by blood-vessels. 2. The umbilical cord, which connects the embryon with the placental portion of the chorion, and the umbilical vesicle, formed from the same layers as the allantois. 3. The amnion, which is the internal layer of the amniotic fold, persisting throughout the whole of fœtal life. 4. The embryon itself.

During the early stages of development of the umbilical vesicle and the allantois, the

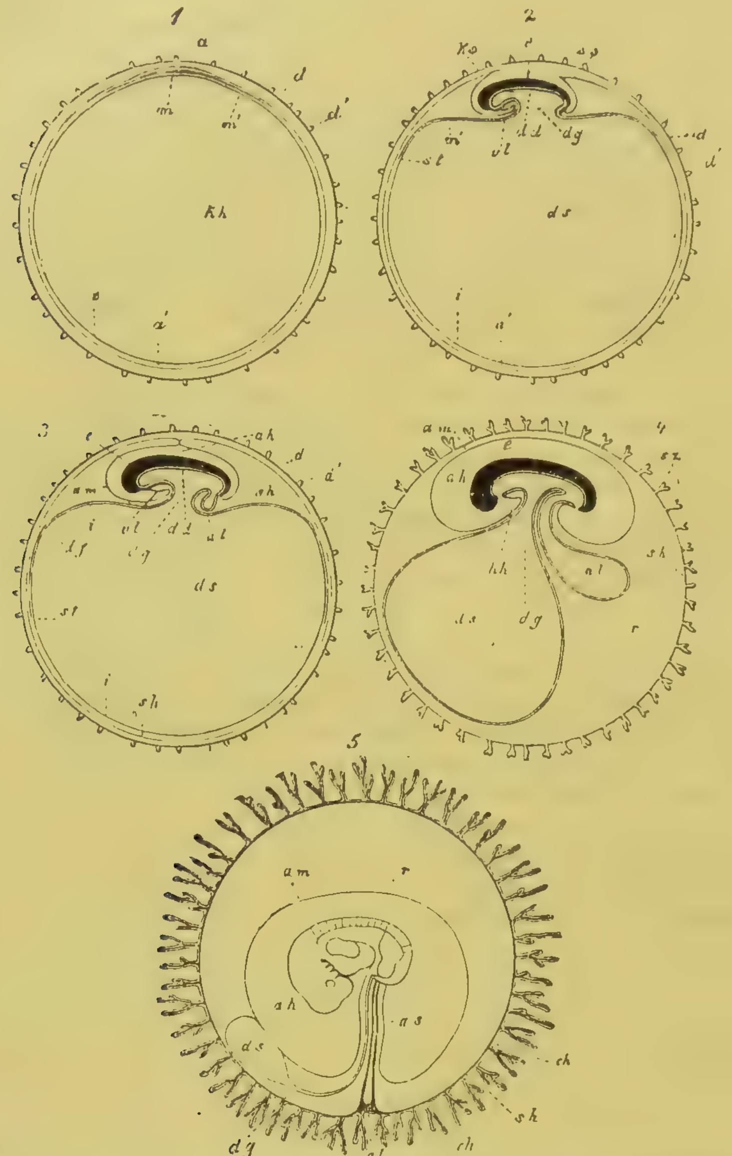


FIG. 291.—*Fire diagrammatic representations of the formation of the membranes in the mammalia.* (Kölliker.)

FIG. 1: *a*, *a'*, external layer of the blastoderm; *d*, vitelline membrane; *d'*, villi on the vitelline membrane; *i*, internal layer of the blastoderm; *m*, *m'*, middle layer.

FIG. 2: *a'*, external layer of the amnion; *d*, *d'*, vitelline membrane; *e*, embryon; *d s*, umbilical vesicle; *v l*, *k s*, *s s*, folds of the amnion; *d d*, *m'*, *s t*, internal layer of the blastoderm; *d d*, connection of the embryon with the umbilical vesicle.

FIG. 3: *d*, *d'*, vitelline membrane; *v l*, internal amniotic layer; *e*, embryon; *a h*, amniotic cavity; *s h*, *s h*, external amniotic layer; *a m*, space between the two layers of the amnion; *d d*, internal layer of the blastoderm; *d f*, *s t*, *i*, walls of the umbilical vesicle; *d g*, omphalo-mesenteric canal; *d s*, cavity of the umbilical vesicle; *a l*, first appearance of the allantois.

FIG. 4: *s h*, external layer of the amnion; *s z*, villi of the external layer of the amnion, which has now become the chorion, the vitelline membrane having disappeared; *h h*, *a m*, internal layer of the amnion; *e*, embryon; *a h*, amniotic cavity; *d g*, omphalo-mesenteric canal; *d s*, cavity of the umbilical vesicle; *a l*, allantois; *r*, space between the two layers of the amnion.

FIG. 5: *c h*, *s h*, *c h*, *a l*, allantois (which has now become the chorion, the external amniotic layer having disappeared), with its villi; *a m*, amnion; *a s*, amniotic covering of the umbilical cord; *r*, space between the amnion and the allantois; *a h*, amniotic cavity; *d s*, umbilical vesicle; *d g*, omphalo-mesenteric canal.

internal amniotic layer, or the true amniotic membrane, is closely applied to the surface of the embryon and is continuous with the epidermis at the umbilicus. It is then separated from the allantois by a layer of gelatinous matter; and in this layer, between the amnion and the allantois, is embedded the umbilical vesicle. At this time, the umbilical cord is short and not twisted. As development advances, however, the inter-membranous gelatinous matter gradually disappears; the cavity of the amnion is enlarged by the production of a liquid between its internal surface and the embryon; and, at about the end of the fourth month, the amnion comes in contact with the internal surface of the chorion. At this time, the embryon floats, as it were, in the amniotic cavity, surrounded by the amniotic fluid. The amnion forms a lining membrane for the chorion; by its gradual enlargement it has formed a covering for the umbilical cord; and, between it and the cord, is the atrophied umbilical vesicle. The amnion then resembles a serous membrane, except that it is non-vascular. It is lined by a single layer of pale, delicate cells of pavement-epithelium, which contain a few fine, fatty granulations. At term, the amnion adheres to the chorion, though it may be separated, with a little care, as a distinct membrane, and may be stripped from the cord. From its arrangement and from the absence of blood-vessels, it is evident that this membrane is simply for the protection of the fœtus and is not directly concerned in its nutrition and development. (See Plate III., Fig. 2, facing page 922.) The gelatinous mass referred to above, situated, during the early periods of intra-uterine life, between the amnion and the chorion, presents a semifluid consistence, and it is marked by the presence of numerous very delicate, interlacing fibres of young connective tissue and fine grayish granulations scattered through its substance. These fibres gradually develop as the quantity of gelatinous matter diminishes and the amnion approaches the chorion, until, finally, it forms a rather soft, reticulated layer, which is sometimes called the membrana media.

Amniotic Fluid.—The process of enlargement of the amnion shows that the amniotic fluid gradually increases in quantity as the development of the fœtus progresses. At term, the entire quantity is variable, being rarely more than two pints or less than one pint. In the early periods of utero-gestation, it is clear, slightly yellowish or greenish, and perfectly liquid. Toward the sixth month, its color is more pronounced, and it becomes slightly mucilaginous. Its reaction is usually neutral or faintly alkaline, though sometimes it is feebly acid in the latest periods. It sometimes contains a small quantity of albumen, as determined by heat and nitric acid; and there is generally a gelatinous precipitate on the addition of acetic acid. The following table, compiled by Robin, gives its chemical composition:

Composition of the Amniotic Fluid.

Water	991·00 to 975·00
Albumen and mucosine	0·82 " 10·77
Urea	2·00 " 3·50
Creatine and creatinine (Scherer, Robin and Verdeil)	not estimated
Lactate of soda (Vogt, Regnauld)	a trace
Fatty matters (Rees, Mack)	0·13 to 1·25
Glucose (Cl. Bernard)	not estimated
Chloride of sodium and chloride of potassium	2·40 to 5·95
Chloride of calcium	a trace
Carbonate of soda	a trace
Sulphate of soda	a trace
Sulphate of potassa (Rees)	a trace
Calcareous and magnesian phosphates and sulphates	1·14 to 1·72

The presence of certain of the urinary constituents in the amniotic fluid has led to the view that the urine of the fœtus is discharged, in greater or less quantity, into the amniotic cavity. Bernard, who is cited in the above table as having determined the presence of sugar in the amniotic fluid, has shown that, in animals with a multiple placenta, the amnion has a glycogenic function during the early part of intra-uterine existence.

With regard to the origin of the amniotic fluid, it is impossible to say how much of it is derived from the general surface of the fœtus, how much from the urine, and how much from the amnion itself, by transudation from the vascular structures beneath this membrane. The quantity is apparently too great, especially in the early months, to be derived entirely from the urine of the fœtus, and there is probably an exudation from the general surface of the fœtus and from the membranes. After the third month, the sebaceous secretion from the skin of the fœtus prevents the absorption of any of the liquid.

An important property of the amniotic fluid is that of resisting putrefaction and of preserving dead tissues. It is stated by Robin to be the best fluid for the preservation of the embryonic tissues, when it is desired to keep them for examination.

Formation of the Umbilical Vesicle.—As the visceral plates, which will be described hereafter, close over the front of the embryon, that portion of the blastoderm from which the intestinal canal is developed presents a vesicle, which is cut off, as it were, from the abdominal cavity, but which still communicates freely with the intestine. This is the umbilical vesicle. On its surface, is a rich plexus of blood-vessels; and this is a very important organ in birds and in many of the lower orders of animals. In the human subject and in mammals, however, the umbilical vesicle is not so important, as nutrition is effected by means of vascular connections between the chorion and the uterus. The vesicle becomes gradually removed farther and farther from the embryon, as development advances, by the elongation of its pedicle, and it is compressed between the amnion and the chorion as the former membrane becomes distended.

When the umbilical vesicle is formed, in the way which we have indicated, it receives two arteries from the two aortæ, and the blood is returned to the embryon by two veins, which open into the vestibule of the heart. These are called the omphalo-mesenteric vessels. At about the fortieth day, one artery and one vein disappear, and, soon after, all vascular connection with the embryon is abolished. At first there is a canal of communication with the intestine, called the omphalo-mesenteric canal. This is gradually obliterated, and it closes at the thirtieth or the thirty-fifth day. The point of communication of the vesicle with the intestine is called the intestinal umbilicus; and, early in the process of development, there is here a true hernia of a loop of intestine. The umbilical vesicle remains as a tolerably prominent structure as late as the fourth or fifth month, but it may often be discovered at the end of pregnancy.

The umbilical vesicle presents three coats; an external, smooth membrane, formed of connective tissue, a middle layer of transparent, polyhedric cells, and an internal layer of spheroidal cells. The membrane, composed of these layers, encloses a pulpy mass, composed of a liquid containing cells and yellowish granulations.

Formation of the Allantois and the Permanent Chorion.—During the early stages of development of the umbilical vesicle, and while it is being shut off from the intestine, there appears an elevation at the posterior portion of the intestine, which rapidly increases in extent, until it forms a membrane of two layers, which is situated between the internal and the external layer of the amnion. This membrane becomes vascular early in the progress of its development, increases in size quite rapidly, and finally completely encloses the internal layer of the amnion and the embryon, the gelatinous mass already described being situated between it and the internal amniotic layer, before this membrane becomes enlarged. While the formation of the two layers of the allantois is quite distinct in certain of the lower orders of animals, in the human subject and in mammals, it is not so easily observed; still there can be no doubt as to the mechanism of its formation, even in the human ovum. Here, however, the allantois soon becomes a single membrane, the two original layers of which cannot be separated from each other. The process of the development of the allantois is shown in the diagrammatic Figure 291 (3, 4, 5).

It is the vascularity of the allantois which causes the rapid development by which it invades and finally supersedes the external layer of the amnion, becoming the permanent chorion, or external membrane of the ovum. At first there are two arteries extending into this membrane from the lower portion of the aorta, and two veins. The two arteries persist and form the two arteries of the umbilical cord, coming from the internal iliac arteries of the fœtus; and the two veins are reduced to one, the umbilical vein, which returns the blood from the placenta to the fœtus. These vessels are connected with the permanent vascular tufts of the chorion.

The development of the allantois cannot be well observed in human ova before the fifteenth or the twenty-fifth day. We have already noted the formation of villosities, first upon the vitelline membrane, and next upon the external amniotic membrane, and we have seen that both of these membranes are temporary structures. As the vascular allantois encroaches upon the external amniotic layer, the villosities become vascular; and, when the allantois becomes the permanent chorion, it is marked by a multitude of compound villi over its entire surface, which give the ovum a shaggy appearance. It is difficult to say whether new villi appear upon the allantois, or whether the villi of the amnion are penetrated by the vessels of the allantois; but it is certain that the true or permanent chorion presents upon its surface vascular villi. As the ovum enlarges, over a certain area surrounding the point of attachment of the pedicle which connects it with the embryon, the villi are developed more rapidly than over the rest of the surface. Indeed, as the egg becomes larger and larger, the villi of the surface outside of this area become more and more scanty, lose their vascularity, and finally disappear. That portion upon which the villi persist and increase in length and in the number of their branches is destined to form connections with the mucous membrane of the uterus, and it constitutes the fœtal portion of the placenta. This change begins at about the end of the second month, and the placenta becomes distinctly limited at about the end of the third month.

FIG. 292.—*Human embryon at the third week, showing villi covering the entire chorion.* (Hæckel.)

It must be remembered that, as the changes progress which result in the formation of the permanent chorion and the limitation of the fœtal portion of the placenta, the formation of the umbilical vesicle and the enlargement of the amnion are also going on. The amnion is gradually becoming distended by the increase in the quantity of amniotic fluid. It reaches the internal surface of the chorion at about the end of the fourth month, extends over the umbilical cord to form its external covering, including the cord of the umbilical vesicle, and the umbilical vesicle itself lies in the gelatinous matter between the two membranes.

At about the beginning of the fifth month, then, the ovum is constituted as follows:

The fœtus floats freely in the amniotic fluid, attached to the placenta by the umbilical cord; the chorion presents a highly-vascular, thickened, and villous portion, the fœtal portion of the placenta; the rest of the chorion is a simple membrane, without villi and without blood-vessels; the amnion lines the internal surface of the chorion and also forms the external covering of the umbilical cord; the umbilical vesicle has become atrophied and has lost its vascularity; the hernia at the point of connection of the umbilical vesicle with the intestine of the fœtus has closed; and, finally, the fœtus has undergone a considerable degree of development.

It now remains for us to study the structure of the umbilical cord, the membranes formed from the mucous membrane of the uterus, or the membranæ deciduæ, and the mode of development and the structure of the placenta.

Umbilical Cord.—From the description we have given of the mode of development of the chorion and the amnion, it is evident that the umbilical cord is nothing more than the pedicle which connects the embryon with that portion of the chorion which enters into the structure of the placenta. It is, indeed, a process of the allantois, in which the vessels eventually become the most important structures. The cord is distinct at about the end of the first month; and, as development advances, the vessels consist of two arteries coming from the body of the fœtus, which are usually twisted from left to right around the single umbilical vein. In addition to the spiral turns of the arteries around the veins, the entire cord may be more or less twisted, probably from the movements of the fœtus.

The fully-developed cord extends from the umbilicus of the fœtus to the central portion of the placenta, in which its insertion is usually oblique; though it may be inserted at other points, and even outside of the border of the placenta, its vessels penetrating this organ from the side. Its usual length, which varies very considerably, is about twenty inches. It has been observed as long as sixty, and as short as seven inches. When the cord is very long, it sometimes presents knots, or it may be wound around the neck, the body, or any of the members of the fœtus; and this can only be accounted for by the movements of the fœtus *in utero*.

The external covering of the cord is a process of the amnion, which, as it extends over the vessels, includes a gelatinous substance (the gelatine of Wharton) which surrounds the vessels and protects them from compression. This gelatinous substance is identical with the so-called membrana intermedia, or the substance included between the amnion and the chorion. The entire cord, covered with the gelatine of Wharton and the amnion, is usually about the size of the little finger. According to Robin, the normal cord will sustain a weight of from ten pounds and ten ounces to twelve pounds and twelve ounces avoirdupois. As the amniotic fluid accumulates and distends the amniotic membrane, it becomes more and more closely applied to the cord. This pressure extends from the placental attachment of the cord toward the fœtus and gradually forces into the abdomen of the fœtus the loop of intestine, which, in the early periods of intra-uterine life, forms an umbilical hernia.

It is generally stated by writers upon embryology that the vessels of the cord present no valves; but recent observations have demonstrated the presence of semilunar folds, both in the vein and in the arteries. These are simple inversions of the walls of the vessels; and they do not exist in pairs, nor do they seem to influence the current of blood. In the arteries, these folds are situated at intervals of from half an inch to two inches, and they are more abundant where the vessels are very contorted. In the vein, the folds are most abundant near the placenta; they are very irregularly placed, and, in a length of four inches, fifteen folds were found. It is not apparent that these folds have any physiological importance.

As the allantois is developed, it presents, in the early stages of its formation, three portions; an external portion, which becomes the chorion, an internal portion, enclosed in the body of the embryon, and an intermediate portion. The intermediate portion, as we have seen, becomes the umbilical cord. As the umbilicus of the fœtus closes around the cord, it shuts off a portion of the allantois contained in the abdominal cavity, which becomes the urinary bladder; but there is a temporary communication between the internal portion and the lower portion of the cord, which is called the urachus. This is generally obliterated before birth and is reduced to the condition of an impervious cord; but it may persist during the whole of intra-uterine life, in the form of a narrow canal, extending from the bladder to the umbilicus, which is closed soon after birth.

Membranæ Deciduæ.—In addition to the two membranes connected with the fœtus, there are two membranes formed from the mucous membrane of the uterus, which are derived from the mother and which serve still farther to protect the ovum. The chorion, as we have just seen, is for the protection of the fœtus; but a portion of this membrane, about one-third of its surface, becomes closely united with a corresponding portion of the uterine mucous membrane, to form the placenta. This organ, which serves for the nutrition of the fœtus, will be described by itself; but, before we can thoroughly comprehend its structure and the process of its development, we must study carefully the formation of the membranæ deciduæ.

As the fecundated ovum descends into the uterus, it is usually invested with a shaggy covering, which is either the permanent chorion or one of the membranes which invests the ovum previous to the complete development of the allantois. At this time, the mucous membrane of the uterus has undergone certain changes by which it is prepared for the reception of the ovum. The changes which this membrane undergoes in menstruation have already been studied. It has been seen that, during an ordinary menstrual period, the membrane has been increased three or four times in thickness and has become more or less rugous. Without being able to state from positive observation the character of the first changes in the uterine mucous membrane preceding the descent of the fecundated ovum—for the opportunities for direct inspection of these parts after fecundation and before the arrival of the ovum are not frequent—it is almost certain that this hypertrophy occurs and progresses. One of the most favorable occasions for observing these early changes in the human subject lately presented itself, and the appearances were minutely described by Reichert. In this case, the ovum was lenticular, measuring nearly one-fourth of an inch in its long and about one-sixth of an inch in its short diameter. It was covered with simple, empty, cylindrical villi, and was estimated to be at from the twelfth to the thirteenth day of its development, dating from fecundation. It was enclosed in the decidua reflexa, and it was thought that this had been accomplished from twenty-four to forty-eight hours before the death of the mother.

According to Reichert, the thickening of the mucous membrane of the uterus which occurs at each menstrual period, in case the ovum be not fecundated, is relieved by a flow of blood and disappears; but, if fecundation take place, the membrane continues to hypertrophy and to prepare itself to enclose the ovum. In this process, when an ovum has been fecundated, there are formed, upon the surface of the mucous membrane, little elevations, or islands, provided with primary and secondary papillæ everywhere except at their borders, where the membrane is smooth and presents the enlarged orifices of the uterine follicles. The ovum observed by Reichert was found embedded in the parenchyma of one of these islands; and, as it was detached, several villi were drawn immediately out from the uterine tubules.

It is now well known that the mucous membrane lining the gravid uterus forms what has been called the decidua vera, and that a portion is reflected over the ovum, to form the decidua reflexa. Reichert is of the opinion that the view entertained by most observers, that the fecundated ovum lodges itself in one of the furrows of the hypertrophied membrane and is finally enclosed by an elevation of the walls of the furrow, cannot be sustained. He thinks that the ovum first becomes attached to one of the "islands;" at the point of attachment, the island does not increase in size as rapidly as at other portions, so that the ovum rests in a cup-shaped depression; and, finally, a growth takes place from the margin of this depression, which extends around and encloses the ovum, presenting a spot where the final closure takes place, called the decidual umbilicus.

We have given the recent views of Reichert thus fully, for the reason that they are based upon the study of a remarkably young ovum and appear to be more exact and definite than any observation hitherto recorded; and we shall adopt this description as representing the early stages of the formation of the membranæ deciduæ.

According to Reichert, the ovum is completely enclosed at the twelfth or the thirteenth day. The mucous membrane lining the uterus becomes the decidua vera; and the border from which the new growth is formed which covers the ovum is the boundary between this and the decidua reflexa. The new growth, springing from this border, envelops the ovum completely and is called the decidua reflexa; and, in this membrane, there is no trace of the uterine tubules.

As development advances, a portion of the decidua vera—the description of which we reserve for the present—undergoes development into the maternal portion of the placenta. The rest of the decidua vera becomes extended, loses its vessels and glands, and is reduced to the condition of a simple membrane. The cylindrical epithelial cells of the mucous membrane of the body of the uterus, soon after fecundation, become gradually exfoliated, and their place is supplied by flattened epithelial scales, of the pavement-variety. This change is effected at from the sixth to the eighth week, and the pavement-cells are then found covering both the decidua vera and the reflexa. The epithelium of the cervix retains its cylindrical character, but most of the cells lose their cilia.

During the first periods of utero-gestation, the two layers of decidua are separated by a small amount of an albuminous and sometimes a sanguinolent fluid; but this disappears at about the end of the fourth month, and the membranes then come in contact with each other. They soon become so closely adherent as to form a single membrane, which is in contact with the chorion. Sometimes, at full term, the membranes of the fœtus can be separated from the decidua; but frequently all of the different layers are closely adherent to each other.

The changes we have just described are not participated in by the mucous membrane of the neck of the uterus. The glands in this situation secrete a semisolid, transparent, viscid mucus, which closes the os and is sometimes called the uterine plug.

Toward the fourth month, a very delicate, soft, homogeneous layer appears over the muscular fibres of the uterus, beneath the decidua vera, which is the beginning of a new mucous membrane. This is developed very gradually, and the membrane is completely restored about two months after parturition.

Development and Structure of the Placenta.—In describing the formation of the membranæ deciduæ and of the chorion, we have necessarily hinted at the mode of development of the placenta. Although there is considerable difference of opinion among anatomists with regard to the exact relations between the vessels of the mother and of the fœtus *in utero*, it is admitted by all that the fœtus derives its nourishment from the maternal blood, and that the placenta is, in addition, a respiratory organ. Reasoning from what we should consider to be the requirements of the fœtus, it would be natural to suppose that the fœtal vessels are bathed in maternal blood; and it is certain that the two sets of vessels have no direct communication with each other. It is also well known that the fœtus has an independent circulation, its heart beating about twice as fast as the heart of the mother. In our description of the placenta, we shall first give the views which we conceive to be correct, and then advance the facts and arguments by which these views are apparently supported.

Beginning with the first development of the placenta, the observation which we have quoted from Reichert, in which, it will be remembered, the tufts of the fœtal chorion were actually drawn out of the tubules of the uterine mucous membrane, seems to demonstrate beyond question the fact of penetration of the villi of the chorion into the maternal tubes. This is a capital point in our view of the mode of development of the placenta; and this cannot be questioned, if we admit the accuracy of Reichert's description. It is certain that the portion of the chorion which eventually becomes attached to the uterus undergoes a much greater degree of development than the rest of the membrane. The villi in this situation become branched and arborescent; they are filled with blood-vessels, while the vascularity in other parts of the chorion disappears; the mucous membrane corresponding to this portion of the chorion also becomes thickened; the tubes in which the villi have penetrated are correspondingly enlarged and branched, and the vessels which surround them are increased in size; and, finally, the union between the villi and the tubes becomes so close that they cannot be separated from each other. It is evident that, if this be the mode of development of the placenta, the maternal portion is formed from a restricted and an hypertrophied part of the mucous membrane of the uterus, and the fœtal portion is simply an exceedingly vascular and villous part of the chorion.

As development advances, the vessels of the maternal portion of the placenta coalesce into great lakes, which communicate freely with the uterine sinuses. In these great cavities, we find the vascular fœtal tufts; and it is easy to understand how transudation of nutritive material and gases can take place from the blood of the mother to the vascular system of the fœtus.

If the above description be correct, we should be able to pass an injection from the uterine sinuses into the maternal portion of the placenta, even as far as its fœtal surface; but this is a point concerning which there has been a great deal of discussion.

In injected specimens of the placenta, when an attempt has been made to fill the maternal as well as the fœtal vessels, the material injected into the uterine vessels has sometimes passed through the entire thickness of the placenta and appeared just beneath the transparent chorion at the fœtal surface of the organ. This appearance, however, has been thought by some writers to be due to extravasation; and many physiologists are of the opinion that the placenta has no maternal portion, that it is entirely a fœtal organ, and that the maternal vessels do not pass beyond the surface by which it is attached to the walls of the uterus. This opinion, however, we believe to be erroneous.

The important point in the determination of the connection of what may be termed the placental maternal sinuses with the vessels of the uterus can be settled by injection of the uterine vessels in cases in which the observation can be made while the placenta is still attached to the uterine walls. Dalton, since 1853, has examined the parts *in situ* in four cases of women who died undelivered at or near the full term of pregnancy, and he adopted the ingenious expedient of filling the uterine vessels with air, by which the course of the injection could be directly observed. This operation is performed in the following manner: The uterus, with its contents, is removed from the body, is carefully opened, and the fœtus is taken out, after dividing the umbilical cord. The parts are then placed under water, the end of a blow-pipe is introduced into one of the divided vessels of the uterine walls, and air is forced in by gentle insufflation. By this process, the venous sinuses of the uterus itself are first filled, next, the deeper portions of the placenta, and finally, "the bubbles of air insinuate themselves everywhere between the fœtal tufts, and appear in the most superficial portions of the placenta, immediately underneath the transparent chorion. If the chorion be now divided at any point by an incision, passing merely through its own thickness, the air, which was confined beneath it in the placental sinuses, will escape, and rise in bubbles to the surface of the water. Such an experiment shows conclusively that the placental sinuses communicate freely with the uterine vessels, occupy the entire thickness of the placenta, and are equally extensive with the tufts of the fœtal chorion." Dalton farther states that the uterine vessels, as they penetrate the placenta, have an exceedingly oblique direction, and that their orifices may be easily overlooked, but can be seen by careful inspection.

We have no doubt with regard to the accuracy of the observations of Dalton, and we conceive that they have settled the question of the existence of a true maternal portion of the placenta. In corroboration of this, in 1864, we examined the uterus, with the placenta attached, of a woman who died in the latter months of pregnancy, in the presence of the late Prof. G. T. Elliot and Prof. J. P. White, and forced air from the uterine sinuses throughout the entire thickness of the placenta, between the fœtal tufts. In view of these facts, concerning which there can be no doubt, it seems unnecessary to discuss the more or less theoretical views of writers who have not made injections of the uterus with the placenta attached. The observations of Dalton have since been confirmed by numerous anatomists, so that we must consider the fact of an intra-placental circulation of maternal blood as definitively established.

Structure of the Fully-developed Placenta.—The placenta of the human subject presents certain differences in its structure at various periods of utero-gestation, most of which have been indicated in treating of its development. At about the end of the third month, the limits of the placenta become distinct, and the organ rapidly assumes the anatomical characters observed after it may be said to be fully developed. It then occupies

Fig. 293.—*Diagrammatic figure, showing the placenta and deciduæ.* (Liégeois.)
c, embryon; i, intestine; p, pedicle of the umbilical vesicle; o, umbilical vesicle; m, m, m, amnion; a', chorion; a, lower end of the umbilical cord; q, q, vascular tufts of the chorion, constituting the fœtal portion of the placenta; n', n, maternal portion of the placenta; n, n, decidua vera; s, decidua reflexa.

about one-third of the uterine mucous membrane, and it is generally rounded or ovoid in form, with a distinct border connected with the decidua and the chorion. It is from seven to nine inches in diameter, a little more than an inch in thickness at the point of penetration of the umbilical cord, slightly attenuated toward the border, and weighs from fifteen to thirty ounces. Its fœtal surface is covered with the smooth amniotic membrane, and its uterine surface, when detached, is rough, and divided into numerous irregular lobes or cotyledons, from half an inch to an inch and a half in diameter. Between these lobes, are membranes, called dissepiments, which penetrate into the substance of the organ, frequently as far as the fœtal surface.

Upon the uterine surface of the placenta, is a thin, soft membrane, sometimes called the decidua serotina. This is merely a portion of the mucous membrane of the uterus situated next the muscular walls, the greater part of it not being thrown off with the placenta. It is composed of amorphous matter, numerous granulations, and colossal cells with enlarged and multiple nuclei. If we scrape the uterine surface of a fresh placenta, these cells appear, upon microscopical observation, very much like the so-called cancer-cells. There has been and is now considerable difference of opinion with regard to the formation of the decidua serotina. Some writers, who do not admit that the placenta has any true maternal portion, regard it as the portion of decidua imprisoned between the chorion and the muscular walls of the uterus; but, if we adopt the view that the placenta is formed in part of the uterine mucous membrane, we must regard the serotina, so called, as simply the deeper portion of this membrane.

Blood-vessels of the Placenta.—The two arteries of the umbilical cord branch upon the fœtal surface of the placenta beneath the amnion and finally penetrate the substance of the organ. The branches of the veins, which are about sixteen in number, converge toward the cord and unite to form the umbilical vein. Upon the uterine surface of the placenta, are numerous oblique openings of the veins which return the maternal blood to the uterine sinuses. There are also numerous small spiral arteries, which pass into the substance of the organ to supply blood to the maternal portion. These are the "curling arteries," described by John Hunter.

If we inject the umbilical arteries, the fluid is returned by the umbilical vein, having passed through the vascular tufts of the fœtal portion of the placenta. According to Farre, the small arteries and the veins of the villi at first communicate through a true capillary plexus; but, toward the end of pregnancy, the capillaries disappear, leaving loops of vessels, "simple, compound, wavy, or much contorted, and in parts varicose."

According to the recent researches of Winkler, there are three kinds of fœtal villi: 1. Those which terminate just beneath the chorion, without penetrating the vascular lacunæ. 2. Longer villi, which hang free in the lacunæ. 3. Long, branching villi, which penetrate more deeply into the placenta, some extending as far as its uterine surface.

The formation of the great vascular lakes of the maternal portion of the placenta has already been described. These, according to Winkler, present numerous trabeculæ, which extend from the uterine to the fœtal surface; and, between these trabeculæ, are numerous exceedingly delicate transverse and oblique secondary trabecular processes. The chorionic villi contain blood-vessels, which we have already described, surrounded by a gelatinous, connective-tissue structure (*Schleimgewebe*), and are generally covered with a layer of nucleated cells of pavement-epithelium.

In parturition, the curling arteries and the veins on the uterine surface of the placenta are torn off, and the placenta then consists of the parts we have just described; the torn ends of these vessels attached to the uterus are closed by the contractions of the surrounding muscular fibres; and the blood which is discharged is mainly derived from the placenta itself. Thus the very contractions which expel the contents of the uterus close the vessels and prevent loss of blood by the mother.

Development of the Embryon.

The product of generation retains the name of ovum until the form of the body begins to be apparent, when it is called the embryon. At the fourth month, about the time of quickening, it is called the fœtus, a name which it retains during the rest of intra-uterine life. The membranes which we have described are appendages developed for the purposes of protection and nutrition; and the embryon itself, in the mammalia, is developed from a restricted portion of the layers of cells resulting from the segmentation of the vitellus.

We have already described the formation of the blastodermic cells and the appearance of the groove which is subsequently developed into the neural canal. At this portion of the ovum, there is a thickening of the blastoderm, which then presents three layers, the middle layer, the thickest and most important, being developed from the opposite surfaces of the external and the internal layer. We have to study, then, the changes which take place in three layers of cells, which we shall call the external, the intermediate, and the internal blastodermic membranes. The earliest stages of development have been studied almost exclusively in the chick, and the processes here observed cannot be assumed to represent exactly the mode of development of the human subject. For this reason, we feel justified in adopting the simplest division of layers, which is into three, and shall not attempt to follow the excessively minute descriptions of the early arrangement of cells, given by some recent observers.

A general idea of the development of certain of the important parts of the embryon will aid us in comprehending the more minute processes and the formation of special organs; and this we can give without reference to the various divisions of the blastodermic layers adopted by different writers. It makes very little difference, indeed, as regards our actual knowledge of development, whether we restrict the external blastodermic membrane to the development of the epidermis, or whether we assume that a portion of it forms the walls of the neural canal. In the latter case, we simply make a thicker external layer at the expense of a portion of the intermediate layer. It is the discussion of such minor points as this, which depend mainly upon observations made upon the chick, that we propose to avoid, in our endeavor to make the description of the first processes of development as simple as possible.

We may assume that the furrow for the spinal canal and its dilated superior portion, the head, have been closed over by the union of the dorsal, or medullary plates behind. At a later period, there has been a growth of the abdominal, or visceral plates, which finally close over the front of the embryon. Now, to adopt, with slight modifications, a simile given by Hermann, we may imagine a young mammal, with a short, straight alimentary canal, taking no account, for the present, of its glandular appendages. We take the entire body as a tube, the caliber of which is the alimentary canal, with walls formed of concentric layers. Counting these layers from within outward, we have first, the mucous membrane; next, the muscular coat of the intestine; then, the visceral serous membrane, the parietal serous membrane, the muscles of the trunk, with the bones; and finally, the integument. All of these layers are developed, to a greater or less degree, simultaneously, from different layers of the blastodermic cells. With the view that we shall adopt, the external blastodermic membrane becomes the epidermis, and the internal blastodermic membrane, the epithelium of the alimentary canal. The intermediate membrane splits into two layers; the outer layer becoming attached to the external blastodermic membrane and forming the muscular layer of the trunk, while the inner layer is connected with the internal blastodermic membrane and contributes to the formation of the viscera. At a later period, the extremities are developed, as solid processes connected with the outer layer of the intermediate membrane and covered by a prolongation of the external blastodermic membrane.

Development of the Cavities and Layers of the Trunk in the Chick.—As an introduction to a description of the development of special organs in the human subject and in mammals, it will be found very useful to study the first stages of development in the chick, by which we can get an idea of the arrangement of the different blastodermic layers, and the way in which they are developed into the different parts of the trunk, with the mode of formation of the great cavities. In doing this, we shall endeavor to describe the figures given by Brücke, which were photographed on wood from large diagrams, made from actual preparations, by Seboth. In this description, we shall take no account of the formation of the membranes.

Fig. 294 illustrates one of the earliest stages of development in the chick. In this figure, the superior layer of dark cells (*b*, *b*) represents the external blastodermic membrane. The inferior layer of dark cells (*d*, *d*) represents the internal blastodermic membrane. The middle layer of lighter cells is the intermediate membrane, which, toward

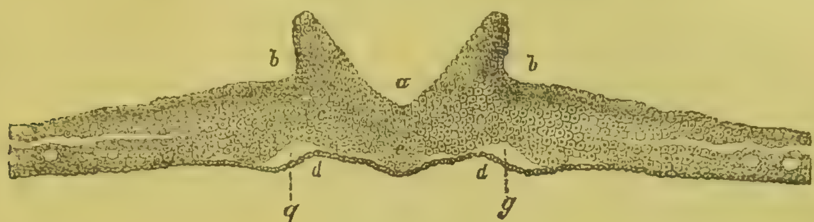


FIG. 294.

the periphery, is split into two layers. This figure represents a transverse section. At *a*, is a transverse section of the groove which is subsequently developed into the canal for the spinal cord. Beneath this groove, is a section of a rounded cord (*e*), the chorda dorsalis. The openings (*g*, *g*) represent the situation of the two aortæ. The other cavities are as yet indistinct in this figure.

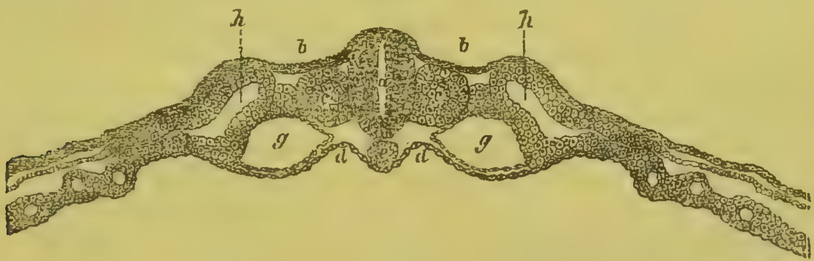


FIG. 295.

Fig. 295 shows the same structures at a more advanced stage of development. The dorsal, or vertebral plates, which bound the furrow (*a*) in Fig. 294, are closed above, and include (*a*) the neural canal. The chorda dorsalis (*e*) is separated from the cells surrounding it in Fig. 294. We have still the external blastodermic membrane (*b*, *b*) and the internal blastodermic membrane (*d*, *d*), presenting various curves which follow the arrangement of the cells of the intermediate layer. By the sides of the boundaries of the neural canal, are two distinct masses of cells (*c*, *c*), which are developed into the vertebræ. Outside of these masses of cells, are two smaller collections of cells, afterward developed into the Wolffian bodies, which will be described farther on. Beneath those two masses, are two large cavities (*g*, *g*), the largest cavities shown in Fig. 295, presenting an irregular form, which are sections of the two primitive aortæ. The two openings (*h*, *h*) become afterward the pleuro-peritoneal cavity.

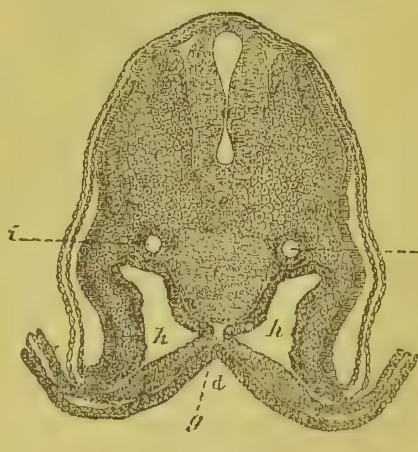


FIG. 296.

In Fig. 296, the parts are still farther developed. The neural canal is represented (*a*) nearly the same as in Fig. 295, with the chorda dorsalis (*e*) just beneath it. A groove, or gutter (*d*) has been formed in front, which is the groove of the intestinal canal. This remains open at this time and is lined by the internal blastodermic membrane. Just above *d*, is a single opening (g), which is formed by the union of the two openings (g, g) in Figs. 294 and 295, and this is the abdominal aorta, which has here become single. The two openings (h, h) represent a section of the pleuro-peritoneal cavity. The outer wall of this cavity is the outer visceral plate, which is developed into the muscular walls of the abdomen. The lower and inner wall is the inner visceral plate, which forms the main portion of the intestinal wall. The outer wall is the outer layer of the intermediate membrane, and the inner wall is the inner layer of the same membrane. The two round orifices (i, i) are sections of the Wolffian ducts.

The figures we have just described, it must be borne in mind, represent transverse sections of the body of the chick, made through the middle portion of the abdomen. In our explanations of these figures, we have not adhered absolutely to the text of Brücke, but have made use of the very elegant semi-diagrammatic illustrations by Waldeyer, whose explanations are remarkably clear and satisfactory. Our explanations, however, particularly those of Fig. 296, are sufficiently extended to enable us to study the development of special organs. The posterior parts, it is seen, are developed first, the situation of the vertebral column being marked soon after the enclosure of the neural canal by the vertebral plates; and, at about the same time, the two aortæ make their appearance, with the first traces of the pleuro-peritoneal cavity. The next organs in the order of development, after the vascular system, are the Wolffian bodies, which are so large and important in the early life of the embryon. The intestinal canal is then a simple groove, and the embryon is entirely open in front. Were we now to follow the process of development farther, we should see that the visceral plates advance and close over the abdominal cavity, as the medullary plates have closed over the neural canal. Thus there would be formed a closed tube, the intestine, lined by the thin, internal blastodermic membrane, the walls of the intestine being formed of the inner layer of the intermediate membrane. This would bring the external layer of the intermediate membrane around the intestine to form the muscular walls of the abdomen, the cavity (Fig. 296, h, h) being the peritoneal cavity, and the external covering being the external blastodermic membrane. At this time, the great Wolffian bodies lie next the spinal column, between the intestine and the abdominal walls, with the single abdominal aorta situated behind the intestine.

Development of the Skeleton, Muscular System, and Skin.

Chorda Dorsalis.—One of the earliest structures observed in the developing embryon is the chorda dorsalis. This is situated beneath the neural canal and extends the entire length of the body. It is formed of a cord of simple cells, and marks the situation of the vertebral column, though itself it is not developed into the vertebræ, which grow around it and encroach upon its substance, until it finally disappears. This structure has been very minutely described by Robin, under the name of the notocorde. In many mammals, the notocorde presents a slight enlargement at the cephalic extremity, which extends to the auditory vesicles and it is somewhat diminished in size at the caudal extremity. By the sides of this cord, are the masses of cells which are eventually developed into the vertebræ. The vertebræ, as they are developed, are formed of temporary cartilaginous structure, gradually extending around the chorda dorsalis, which then occupies the axis of the spinal column. Between the bodies of the vertebræ, the chorda dorsalis presents regular enlargements, surrounded by a delicate membrane. As ossification of the spinal column advances, that portion of the chorda dorsalis which is surrounded by the bodies of the vertebræ disappears, leaving the enlargements between the vertebræ distinct. These enlargements, which are not permanent, are gradually invaded by fibrous tissue, their gelatinous contents disappear, and the intervertebral disks, composed of fibro-cartilaginous structure, remain. These disks are permanent between the cervical, the dorsal, and the lumber vertebræ; but they eventually disappear from between the different parts of the sacrum and coccyx, as these are consolidated, this occurring, in the human subject, at from the ninth to the twelfth year. The processes of development just described are represented in Fig. 297.

Vertebral Column, etc.—In Figs. 295 and 296 (*c, c*), are seen the two masses of cells, situated by the sides of the neural canal, which are destined to be developed into the vertebræ. These cells extend around and encroach upon the chorda dorsalis and form the bodies of the vertebræ. They also extend over the neural canal, closing above, and these processes are called the medullary, or dorsal plates. Sometimes the dorsal plates fail to close at a certain point in the spinal column, and this constitutes the malformation known as spina bifida. From the sides of the bodies of the vertebræ, the various processes of these bones are formed. As the spinal column is developed, its lower portion presents a projection beyond the pelvis, which constitutes a temporary caudal appendage, curved toward the abdomen; but this no longer projects after the bones of the pelvis are fully developed. At the same time, the entire vertebral column is curved toward the abdomen, and it is twisted upon its axis from left to right, so that the anterior face of the pelvis presents a right angle to the

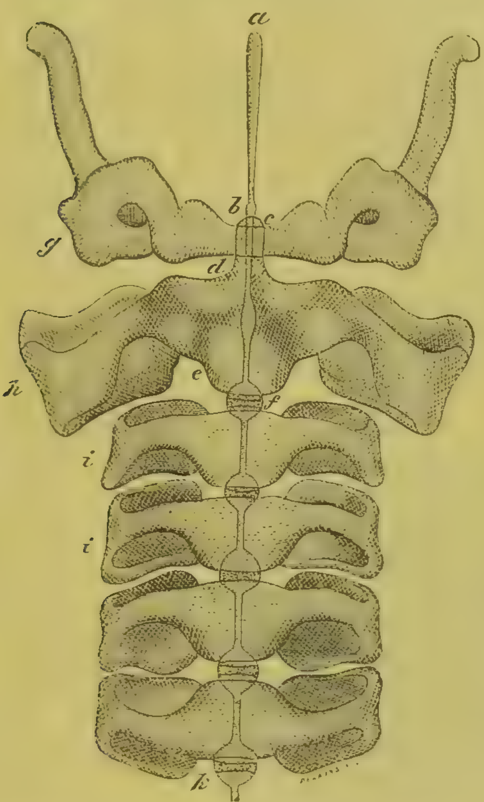


Fig. 297.—*The first six cervical vertebræ of the embryon of a rabbit one inch in length.* (Robin.)

a, b, cephalic portion of the notocorde exposed by the removal of the cartilage; *b*, portion of the chorda dorsalis slightly enlarged, which, in this embryon, was situated between the atlas and the occipital bone; *c*, odontoid process; *d*, base of the odontoid process; *e*, inferior, or second part of the body of the axis; *f, k*, enlargements of the chorda dorsalis between the vertebræ; *g*, cartilage of the lateral portion of the atlas; *h*, lateral portion of the axis; *i, i*, transverse apophyses of vertebræ.

Fig. 298.—*Human embryo, about one month old, showing the large size of the head and upper parts of the body, the twisted form of the spinal column, the rudimentary condition of the upper and lower extremities, and the rudimentary tail at the end of the spinal column.* (Dalton.)

upper part of the body; but, as the inferior extremities and the pelvis become developed, the spine becomes straight. The vertebræ make their appearance first in the middle of the dorsal region, from which point, they rapidly extend upward and downward, until the spinal column is complete.

At the base of the skull, on either side of the superior prolongation of the chorda dorsalis, are two cartilaginous processes, which are developed into the so-called cranial vertebræ. In this cartilaginous mass, three ossific points appear, one behind the other. The posterior point of ossification is for the basilar portion of the occipital bone, which is developed in the same way as one of the vertebræ; the middle point is for the posterior portion of the sphenoid; and the anterior point is for the anterior portion of the sphenoid. The frontal bone, the parietal bone, the temporal bone, and a portion of the occipital bone are developed from the connective tissue, without the intervention of pre-existing cartilaginous structure. The development of the face will be described separately. At the time when the vertebræ are being developed, with their laminæ and their spinous and transverse processes, the ribs extend over the thorax, and the clavicle, scapula, and sternum make their appearance.

At about the beginning of the second month, four papillary prominences, which are the first traces of the arms and legs, appear on the body of the embryon. These progressively increase in length, the arms appearing near the middle of the embryon, and the legs, at the lower portion. Each extremity is divided into three portions, the arm, forearm, and hand, for the upper extremities, and the thigh, leg, and foot, for the lower extremities. At the end of each extremity, there are, finally, divisions into the fingers and toes, with the various cartilages and bones of all of these parts, and their articulations. (See Plates I. and II., Figs. D and H, facing page 920.)

Very early in intra-uterine life, the skeleton, which is at first entirely cartilaginous, begins to ossify, from little bony points which appear in the cartilaginous structure. The first points appear at nearly the same time (about the beginning of the second month) in the clavicle and the upper and the lower jaw. Similar ossific points, which gradually extend, are also seen in other parts, the head, ribs, pelvis, scapula, metacarpus, and metatarsus, and the phalanges of the fingers and toes. At birth, the carpus is entirely cartilaginous, and it does not begin to ossify until the second year. The same is true of the tarsus, except the calcaneum and astragalus, which ossify just before birth. The pisiform bone of the carpus is the last to take on osseous transformation, this occurring at from the twelfth to the fifteenth year. As ossification progresses, the deposits in the various ossific points gradually extend until they reach the joints, which remain incrusted with the permanent articular cartilage.

While the skeleton is being thus developed, the muscles are formed from the outer layer of the intermediate blastodermic membrane, and the visceral plates close over the thorax and abdomen in front, leaving an opening for the umbilical cord. The various tissues of the external parts, particularly the muscles, begin to be distinct at the end of the second month. The deep layers of the dorsal muscles are the first to be distinguished; then, successively, the long muscles of the neck, the anterior straight muscles of the head, the straight and transverse muscles of the abdomen, the muscles of the extremities, the superficial muscles of the back, the oblique muscles of the abdomen, and the muscles of the face.

The skin appears at about the beginning of the second month, when it is very delicate and transparent. At the end of the second month, the epidermis may be distinguished. The sebaceous follicles are developed at the third month; and, at about the fifth month, the surface is covered with their secretion mixed with desquamated epithelium. This cheesy substance constitutes the vernix caseosa. At the third month, the nails make their appearance, and the hairs begin to grow at about the fifth month. The sudoriparous glands first appear at about the fifth month, by the formation of flask-like processes of the true skin, which are gradually elongated and convoluted, until they are fully developed only a short time before birth.

Development of the Nervous System.

We have seen, in studying the development of the spinal column, how the dorsal, or medullary plates close over the groove for the neural canal. In the interior of this canal, the cerebro-spinal axis is developed, by cells, which gradually encroach upon its caliber, until we have remaining only the small central canal of the spinal cord, communicating with the ventricles of the brain. As the nervous tissue is developed in the interior of the neural canal, there is a separation of the histological elements at the surface, to form the membranes. The dura mater and the pia mater are formed first, appearing at about the end of the second month, while the arachnoid is not distinct until the fifth month. The nerves are not produced as prolongations from the cord into the various tissues, nor do they extend from the tissues to the cord; but they are developed, in each tissue, by a separation of histological elements from the cells of which the parts are originally constituted, which at first appear to be identical in their morphological characters. The nerves of the sympathetic system are developed in the same way.

The mode of development of the spinal cord is thus sufficiently simple; but, with the growth of the embryon, we observe dilatations at the superior and at the inferior extremities of the neural canal. The cord is uniform in size in the dorsal region, marked only by the regular enlargements at the sites of origin of the spinal nerves; but we soon observe an ovoid dilatation below, which forms the lumbar enlargement, from which the nerves are given off to the inferior extremities, and the brachial enlargement above, where the nerves of the superior extremities take their origin. At the same time, there is a more marked dilatation of the canal at its cephalic extremity. Here, a single enlargement appears, which is soon divided into three vesicles, called the anterior, middle, and posterior cerebral vesicles. These become more and more distinct as development advances. The formation of these parts is illustrated in Fig. 299, taken from Wagner, and made more distinct by Longet, as they are drawn upon a black ground. This figure, in C, shows the projections, on either side, of the vesicles which are eventually developed into the nervous portions of the organ of vision.

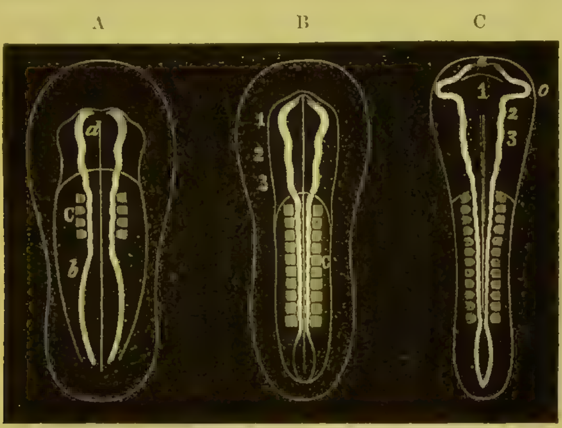


FIG. 299.—*Development of the nervous system of the chick* (Longet.)

A, the two primitive halves of the nervous system, twenty-four hours after incubation; B, the same, thirty-six hours after; C, the same, at a more advanced stage. c, the two primitive halves of the vertebræ; *d*, anterior dilatation of the neural canal; *b*, posterior dilatation (the lumbar enlargement); 1, 2, 3, anterior, middle, and inferior cerebral vesicles; *a*, slight flattening of the anterior cerebral vesicle; *o*, formation of the ocular vesicles.

The three cerebral vesicles now undergo farther changes. The superior, which we may call the first primitive vesicle, enumerating them from above downward, is soon divided into two secondary vesicles, the anterior of which becomes the cerebral hemispheres, and the posterior, the optic thalami, which are eventually covered, by the greater relative development of the hemispheres. The middle, or second primitive vesicle, does not undergo division and is developed into the tubercula quadrigemina, or centres of vision. The posterior, or third primitive vesicle, is divided into two secondary vesicles, the anterior of which becomes the cerebellum, and the posterior, which is covered by the anterior, the medulla oblongata and the pons Varolii. While this division of the primitive cerebral vesicles is going on, the entire chain of encephalic ganglia becomes curved from behind forward, forming three prominent angles. The first of these angles or prominences (*e*, Fig. 300, A, B, C), counting from before backward, is formed by a projection of the tubercula quadrigemina, which, at this time, constitute the most projecting portion of the encephalic mass; the second prominence (*c*, Fig. 300), situated behind the tubercula quadrigemina, is formed by the projection of the cerebellum; the third (*d*, Fig. 300, A, B, C), is the bend of the superior portion of the spinal cord. These projections and the early formation of certain parts of the encephalon in the human subject are illustrated in Fig. 300.

The cerebrum, as we have just seen, is developed from the anterior division of the first primitive cerebral vesicle. The development of this part is more rapid in its lateral portions than in the median line, which divides the cerebrum imperfectly into two lateral halves, forming, in this way, the great longitudinal fissure. At the same time, by the rapid development of the posterior portion, it extends over the optic thalami, the corpora quadrigemina, and the cerebellum. Up to the end of the fourth month, the hemispheres are smooth on their surface; but they then begin to present large depressions, following folds of the pia mater, which are the first convolutions, these increasing rap-

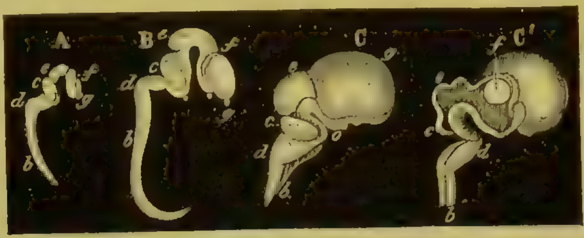


FIG. 300.—*Development of the spinal cord and brain of the human subject.* (Longet.)

A, brain and spinal cord of an embryon of seven weeks; lateral view.
B, the same, from an embryon farther advanced in development; *b*, spinal cord; *d*, enlargement of the spinal cord with its anterior curvature; *c*, cerebellum; *e*, tubercula quadrigemina; *f*, optic thalamus; *g*, cerebral hemispheres.
C, brain and spinal cord of an embryon of eleven weeks; *b*, spinal cord; *d*, enlargement of the spinal cord, with its anterior curvature; *c*, cerebellum; *e*, tubercula quadrigemina; *g*, cerebral hemispheres; *o*, optic nerve of the left side.
C′, the same parts in a vertical section in the median line from before backward; *b*, membrane of the spinal cord turned backward; *d*, second curvature of the upper portion of the spinal cord, which has become thickened and constitutes the peduncles of the cerebrum; *e*, tubercula quadrigemina; *f*, optic thalami covered by the hemispheres.

idly in number and complexity, especially after the seventh month. The septum lucidum is then formed by an elevation of nervous matter from the base, which divides the lower portion of the space left between the hemispheres as they ascend, and forms the two lateral ventricles. At the base of these, are developed the corpora striata. The septum lucidum is formed of two laminæ, with a small space between them, which is the cavity of the fifth ventricle. The posterior division of this first primitive vesicle forms the optic thalami. These become separated in front into two lateral halves, but they remain connected together at their posterior portion, which becomes the posterior commissure. The central canal of the cord is prolonged upward between the optic thalami, and forms the third ventricle, which is covered by the hemispheres.

The second, or middle cerebral vesicle becomes filled with medullary substance, extends upward, and forms the peduncles of the cerebrum, the upper portion being divided to form the tubercula quadrigemina.

The anterior portion of the third primitive vesicle is developed into the cerebellum, the convolutions of which appear at about the fifth month. Its posterior portion forms the medulla oblongata, in the substance of which is the fourth ventricle, communicating with the third ventricle by a little canal, the aqueduct of Sylvius, which is left in the development of the middle vesicle. At about the fourth month, there is a deposition of nervous matter in front and above, forming the pons Varolii.

In Fig. 299 (*C*, *o*), it is seen that the vesicles for the organs of vision appear very early, as lateral offshoots of the anterior cerebral vesicle. These gradually increase in size and advance anteriorly, as development of the other parts progresses. We shall see, when we come to study the development of the face, that the eyes are situated at first at the sides of the head, gradually approaching the anterior portion. At the extremity of each of these lateral prolongations, a rounded mass appears, which becomes the globe of the eye. The superficial portions of the globe are developed into the sclerotic and the cornea, which seem to be formed of a process from the dura mater. The pedicle attached to the globe becomes the optic nerve. The iris is developed at about the seventh week, and is at first a simple membrane, without any central opening. As the pupil appears, it is closed by a vascular membrane—which probably belongs to the capsule of the crystalline lens—called the pupillary membrane. This membrane gradually disappears by an atrophy extending from the centre to the periphery. It attains its maximum of development at the sixth month and disappears at the seventh month. The vitreous humor is formed of the fluid contents of the optic vesicle. The crystalline lens is regarded as a product of the tegumentary layer. At the tenth week, we observe the beginning of the formation of the eyelids. These meet at about the fourth month and adhere together by their edges. In many mammals, the eyelids remain closed for a few days after birth; but they become separated in the human subject in the later periods of fœtal life.

It is probable that the vesicle which becomes developed into the internal ear is formed independently; at least, cases have been observed in which there was congenital absence of the auditory nerves, the parts of the internal ear being perfect. Soon after the formation of the auditory vesicle, however, it communicates with the third primitive cerebral vesicle, the filament of communication being developed into the auditory nerve.

The auditory vesicle, which appears subsequently to the organ of vision, is eventually developed into the vestibule. The next formations are the arches, or diverticula, which constitute the semicircular canals. The membranous labyrinth appears long before the osseous labyrinth; and it has been found perfectly developed at three months. The bones of the middle ear, which have no connection, in their development, with the nervous system, but which it is convenient to mention here, are remarkable for their early appearance. They appear at the beginning of the third month and are as large in the fœtus at term as in the adult. A remarkable anatomical point with relation to these structures is the existence of a cartilage, attached to the malleus on each side and extending from this bone along the inner surface of the lower jaw, the two cartilages meeting and uniting in the median line to form a single cord. "This cartilage now ossifies, although, in the commencement, it forms most of the mass of the bone; it disappears at the eighth month." (Meckel.) This curious structure is known as the cartilage of Meckel.

There are no special points for description in the development of the olfactory lobes, which is very simple. These are offshoots from the first cerebral vesicle, appearing at the inferior and anterior part of the cerebral hemispheres, a little later than the parts connected with vision and audition. The vesicles themselves become filled with ganglionic matter, and constitute the olfactory bulbs, their pedicles being the so-called olfactory nerves, or commissures. The development of some of the parts of the central nervous system is illustrated in Plates I. and II., facing page 920.

As far as the functions of the nervous system of the fœtus are concerned, it is probable that they are restricted mainly to reflex phenomena depending upon the action of the spinal cord, and that perception and volition hardly exist. It is probable that many reflex movements take place *in utero*. When a fœtus is removed from the uterus of an animal, even during the early periods of pregnancy, movements of respiration occur, a fact which we have often demonstrated to medical classes; and it is well known that efforts of respiration sometimes occur within the uterus. This we believe to be a reflex action excited by the want of oxygen in the tissues, when the placental circulation is interrupted. We have already discussed these phenomena in connection with the subject of respiration.

Development of the Alimentary System.

The intestinal canal is the first formation of the alimentary system. As we have already seen, this is at first open in the greatest part of its extent, presenting, at either extremity of the longitudinal gutter, in front of the spinal column, a rounded, blind extremity, which is closed over in front for a short distance. The closure of the abdominal plates then extends laterally and from the two extremities of the intestine, until we have only the opening remaining for the passage of the umbilical cord and the pedicle of the umbilical vesicle. There is at first an open communication between the lower part of the intestinal tube and the allantois, which forms the canal known as the urachus; but that portion of this communication which remains enclosed in the abdominal cavity becomes separated from the urachus, is dilated, and eventually forms the urinary bladder. When the bladder is first shut off, it communicates with the lower portion of the intestine, which is called the cloaca; but it finally loses this connection and presents a special opening, the urethra.

As development advances, the intestine grows rapidly in length and becomes convoluted. It is held loosely to the spinal column by the mesentery, a fold of the peritoneum, this membrane being reflected along the walls of the abdominal cavity. In the early stages of development, a portion of the intestine protrudes at the umbilicus, where the first intestinal convolution appears; and sometimes there is a congenital hernia of this kind at birth, which usually disappears under the influence of gentle and continued pressure. An illustration of this is given in Fig. 301. This protrusion, in the normal process of development, is gradually returned into the abdomen, as the cavity of the pedicle of the umbilical vesicle is obliterated, at about the tenth week.

FIG. 301.—*Fœtal pig, showing a loop of intestine, forming an umbilical hernia.* From a specimen in the possession of Prof. Dalton. From the convexity of the loop, a thin filament is seen passing to the umbilical vesicle, which is here flattened into a leaf-like form.

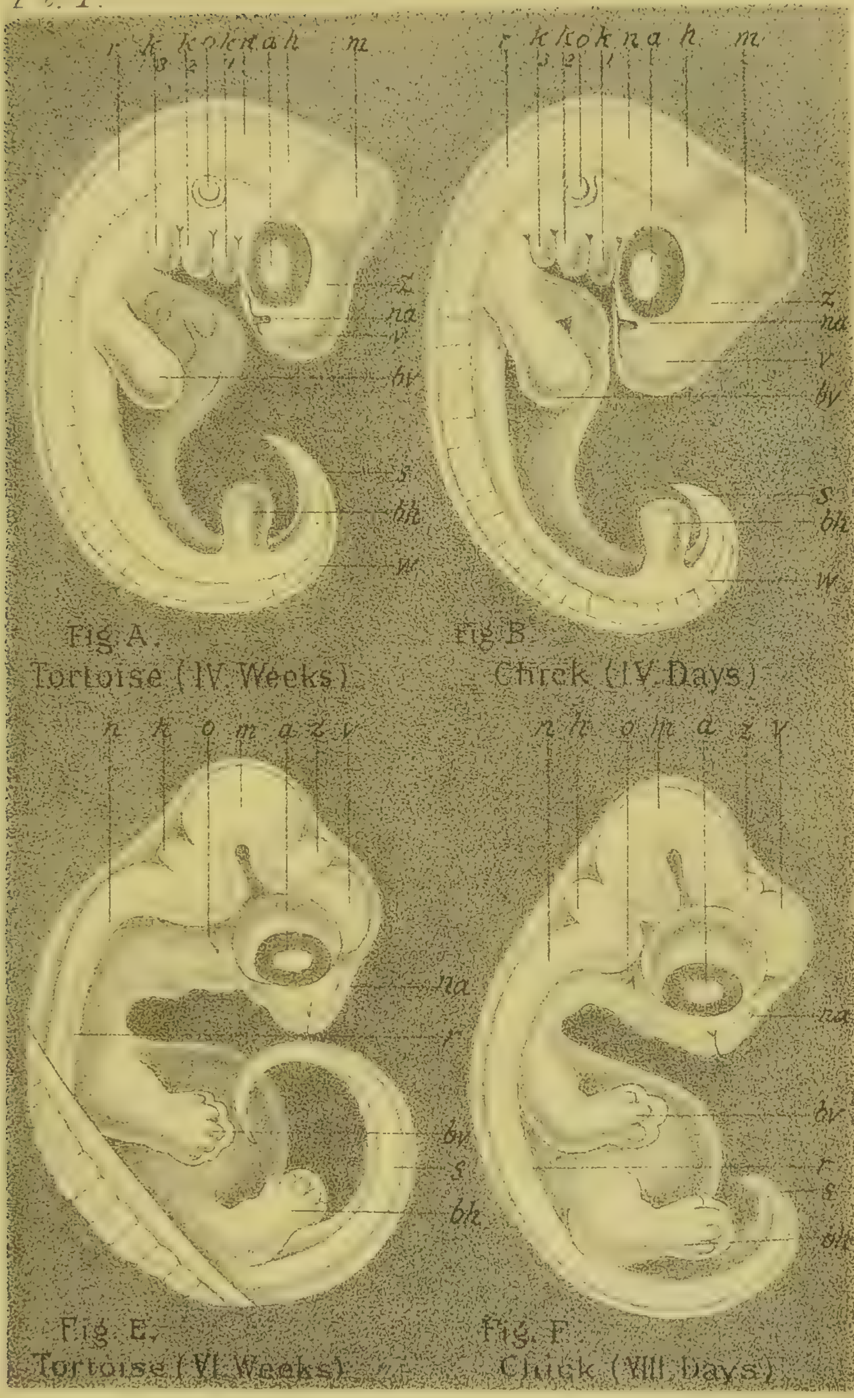
At the upper part of the abdominal cavity, the alimentary canal presents two lateral projections, or pouches. The one on the left side, as it increases in size, becomes the greater pouch of the stomach, and the one on the right side, the lesser pouch.

At a short distance below the attachment of the pedicle of the umbilical vesicle to the intestine, there appears a rounded diverticulum, which is eventually developed into the cæcum, or the commencement of the larger intestine. The cæcum gradually recedes from the neighborhood of the umbilicus, which is its original situation, and finally becomes fixed, by a shortening of the mesentery, in the right iliac region. As the cæcum, or caput coli, is developed, it presents a conical appendage, which is at first fully as large as the small intestine and is relatively longer than in the adult. During the fourth week, this appendage becomes relatively smaller and more or less twisted, forming the appendix vermiformis. At the second month, the cæcum, or caput coli, as we have seen, is at the umbilicus, and the large intestine extends in a straight line toward the anus; at the third month, it is situated at about the middle of the abdomen; and it gradually descends, until it reaches the right iliac region at about the seventh month. Thus, at the second month, there is only a descending colon; the transverse colon is formed at the third month; and the ascending colon, at the fifth month. The ileo-cæcal valve appears at the third month; the rectum, at the fourth month; and the sigmoid flexure of the colon, at the fifth month. During this time, the large intestine increases more rapidly in diameter than the small intestine, while the latter develops more rapidly in its length.

In the early stages of development, the surface of the intestines is smooth; but villi appear upon its mucous membrane during the latter half of intra-uterine existence. These are found at first both in the large and the small intestine. At the fourth month, they become shorter and less numerous in the large intestine, and they are lost at about the eighth month, when the projections which bound the sacculi of this portion of the intestinal canal make their appearance. The valvulæ conniventes appear, in the form of slightly-elevated, transverse folds, in the upper portion of the small intestine. The villi of the small intestine are permanent.

Germs or Embryos

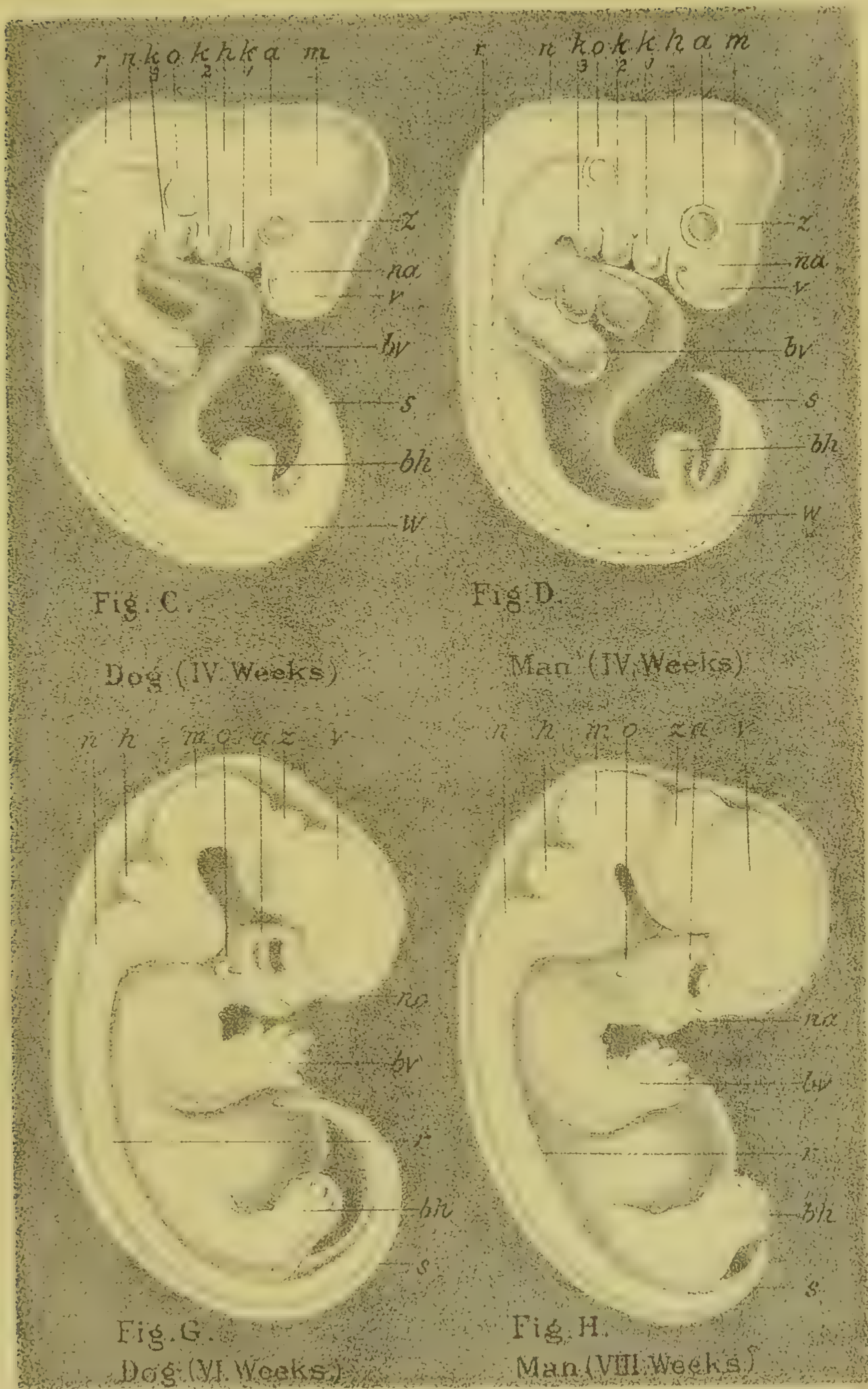
Pl. I.



Figs. *A, B, E, F.*—*v*, anterior cerebral hemispheres; *z*, optic thalami, *m*, tubercula quadrigemina; *h*, cerebellum; *n*, pons Varolii; *r*, spinal cord; *w*, spine; *s*, tail; *a*, eyes; *na*, nose; *o*, ear; k_1, k_2, k_3, visceral arches; *bv*, anterior extremity; *bh*, posterior extremity. (Haeckel.)

of four Vertebrates.

Pl. II.



FIGS. *C*, *D*, *G*, *H*.—*v*, anterior cerebral hemispheres; *z*, optic thalami; *m*, tubercula quadrigemina; *h*, cerebellum; *n*, pons Varolii; *r*, spinal cord; *w*, spine; *s*, tail; *a*, eyes *na*, nose; *o*, ear; k_1, k_2, k_3, visceral arches; *bv*, anterior extremity; *bh*, posterior extremity. (Haeckel.)

The mesentery is first formed of two perpendicular folds, attached to the sides of the spinal column. As the intestine undergoes development, a portion of the peritoneal membrane extends in a quadruple fold from the stomach to the colon, to form the great omentum, which covers the small intestine in front.

As the head undergoes development, a large cavity appears, which is eventually bounded by the arches that are destined to form the different parts of the face. This is the pharynx. It is entirely independent, in its formation, of the intestinal canal, the latter terminating in a blind extremity at the stomach; and, between the pharynx and the stomach, there is at first no channel of communication. The anterior portion of the pharynx presents, during the sixth week, a large opening, which is afterward partially closed in the formation of the face. The rest of this cavity remains closed until a communication is effected with the œsophagus. The œsophagus appears in the form of a tube, which finally opens into the pharynx above and into the stomach below. At this time, there is really no thoracic cavity, the upper part of the stomach is very near the pharynx, the œsophagus is short, the rudimentary lungs appear by its sides, and the heart lies just in front. As the thorax is developed, however, the œsophagus becomes longer, the lungs increase in size, and finally the diaphragm shuts off its cavity from the cavity of the abdomen. The growth of the diaphragm is from its periphery to the central portion, which latter gives passage to the vessels and the œsophagus. Sometimes, when this closure is incomplete, we have the malformation known as congenital diaphragmatic hernia.

The development of the anus is sufficiently simple. At first, as we have seen, the intestine terminates below in a blind extremity; but, at about the seventh week, a longitudinal slit appears below the external organs of generation, by which the rectum opens. This is the anus. It is not very unusual to observe an arrest in the development of this opening, the intestine terminating in a blind extremity, a short distance beneath the integument. This constitutes the malformation known as imperforate anus, a deformity which can usually be relieved, without much difficulty, by a surgical operation, if the distance between the rectum and the skin be not too great. The opening of the anus appears about a week after the opening of the mouth, at or about the seventh week.

The rudiments of the liver appear very early, and, indeed, at the end of the first month, this organ has attained an enormous size. Two projections, or buds, appear on either side of the intestine, which form the two principal lobes of the liver. This organ is at first symmetrical, the two lobes being of nearly the same size, with a median fissure. One of these prolongations from the intestine becomes perforated and forms the excretory duct, of which the gall-bladder, with its duct, is an appendage. During the early part of fœtal life, the liver occupies the greatest part of the abdominal cavity. According to Burdach, its weight, in proportion to the weight of the body at different ages, is as follows: At the end of the first month, 1 to 3; at term, 1 to 18; in the adult, 1 to 36. Its structure is very soft during the first months, and it is only at about the fourth or fifth month that it assumes one of its most important functions, viz., the production of sugar. As development advances, and as the relative size of the liver gradually diminishes, its tissue becomes more solid.

The pancreas appears at the left side of the duodenum, by the formation of two ducts leading from the intestine, which branch and develop glandular structure at their extremities. The spleen is developed, about the same time, at the greater curvature of the stomach. This organ is abundantly supplied with blood-vessels, but it has no excretory duct. The spleen becomes distinct during the second month.

There is no reason to believe that any of the digestive fluids are secreted during intra-uterine life. The stomach, at least, never contains, at this time, an acid secretion. At birth, the intestine contains a peculiar substance, called meconium, which will be described farther on. Cholesterine, an important constituent of the bile, is found in the meconium in large quantity, but its function is connected exclusively with excretion.

Development of the Respiratory System.

On the anterior surface of the membranous tube which becomes the œsophagus, an elevation appears, which soon presents an opening into the œsophagus, the projection forming, at this time, a single, hollow *cul-de-sac*. This opening becomes the rima glottidis, and the single tube with which it is connected is developed into the trachea. At the lower extremity of this tube, a bifurcation appears, terminating first in one, and afterward, in several *culs-de-sac.* The bifurcated tube constitutes, after the lungs are developed, the primitive bronchi, at the extremities of which are the branches of the bronchial tree. As the bronchi branch and subdivide, they extend downward into what becomes eventually the cavity of the thorax. The pulmonary vesicles, according to Burdach, are developed before the trachea. The lungs contain no air at any period of intra-uterine life, and receive but a small quantity of blood; but, at birth, they become distended with air, are increased thereby in volume, and receive all the blood from the right ventricle. This process of development is illustrated in Fig. 302. The lungs appear, in the human embryon, during the sixth week. The two portions into which the original bud is bifurcated constitute the true pulmonary structure, and the formation of the trachea and bronchial tubes occurs afterward and is secondary. We have indicated the pulmonary structure as branching processes from the bronchial tubes, merely for convenience of description.

FIG. 302.—*Formation of the bronchial ramifications and of the pulmonary cells.—A, B, development of the lungs, after Rathke; C, D, histological development of the lungs, after J. Müller.* (Longet.)

Development of the Face.

The development of the face in the embryon of mammals is somewhat complex, but it is peculiarly interesting, as its study enables us to comprehend the manner in which various very common malformations of the face and palate are produced. The anterior portion of the embryon, as we have seen in studying the development of the trunk, remains open in front long after the medullary plates have met at the back and enclosed the neural canal. The common cavity of the thorax and abdomen is closed by the growth of the visceral plates, which meet in front. These are projecting plates of the intermediate blastodermic layer, which gradually extend forward from the vertebral column. At the same time that the visceral plates are thus closing over the thorax and abdomen, four distinct, tongue-like projections appear, one above the other, by the sides of the neck. These are called the visceral arches, and the slits between them are called the visceral clefts.[1] The first three arches, enumerating them from above downward, correspond, in their origin, to the three primitive cerebral vesicles. The fourth arch, which is not enumerated by some authors, who recognize but three arches, corresponds to the superior cervical vertebræ. Of these four arches, the first is the most important, as its development, in connection with that of the frontal process, forms the face and the malleus and incus of the middle ear. The second arch forms the lesser cornua of the hyoid bone, the stapes, and the styloid ligament. The third arch forms the body and the greater cornua of the hyoid. The fourth arch forms the larynx. The first cleft, situated between the first and the second arch, becomes obliterated in front by a deposition of plastic matter, but an opening remains by the side, which forms, externally, the external

[1] These arches correspond to the branchial vascular arches, which will be fully described in connection with the development of the circulatory system.

Pl. III.

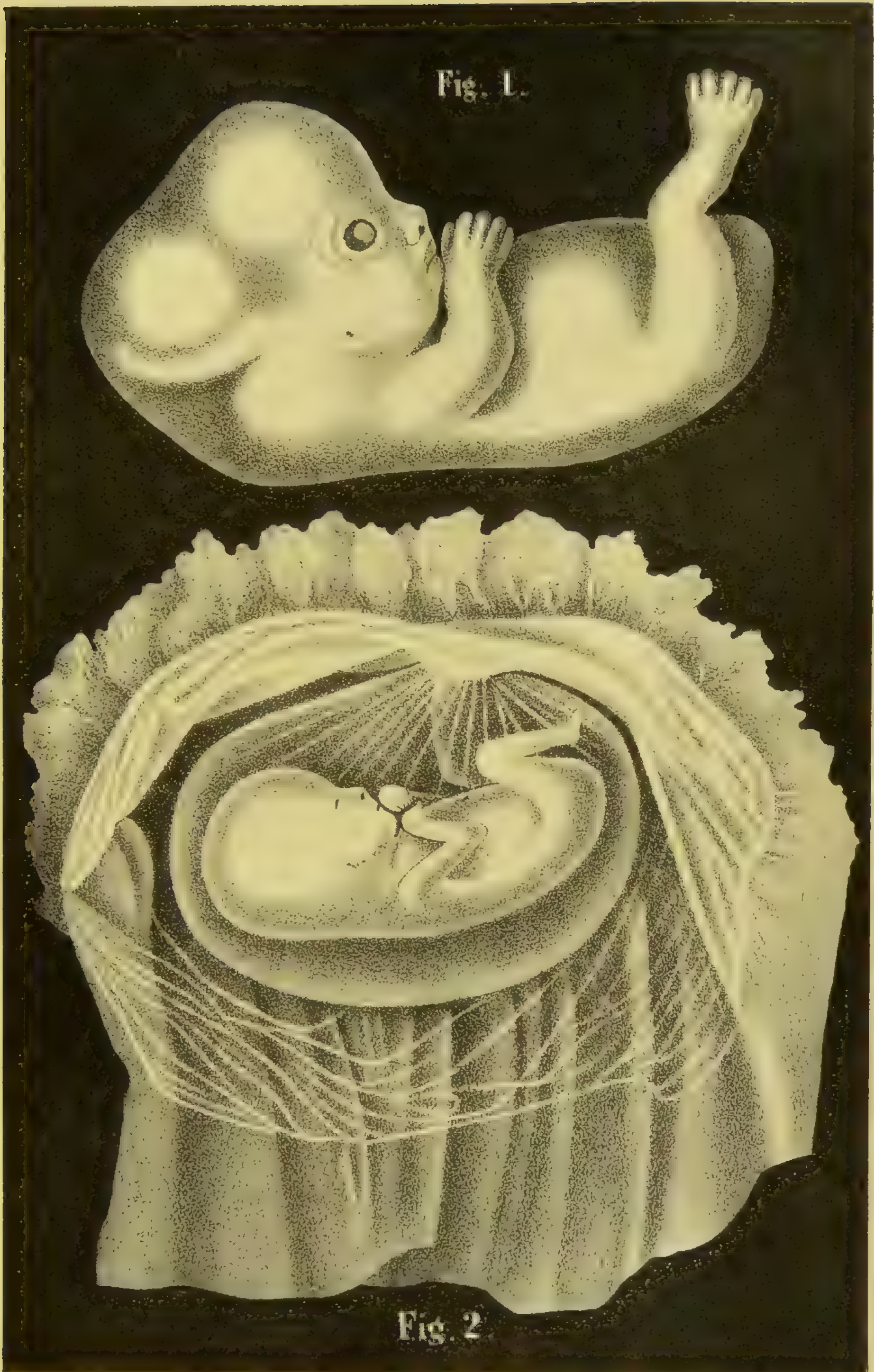


FIG. 1.—*Human embryon, at the ninth week, removed from the membranes; three times the natural size.* (Erdl.)

FIG. 2.—*Human embryon, at the twelfth week, enclosed in the amnion; natural size.* (Erdl.)

auditory meatus, and internally, the tympanic cavity and the Eustachian tube. The other clefts become obliterated as the arches advance in their development.

From the above sketch, it is seen that the face and the neck are formed by the advance and closure in front of projections from behind, in the same way as the cavities of the thorax and abdomen are closed; but the closure of the first visceral arch is complicated by the projection, from above downward, of the frontal, or intermaxillary process, and by the formation of several secondary projections, which leave certain permanent openings, forming the mouth, nose, etc. These processes of development, we shall now attempt to follow.

In the very first stages of development of the head, there is no appearance of the face. The cephalic extremity consists simply of the cerebral vesicles, the surface of this enlarged portion of the embryon being covered, in front as well as behind, by the external blastodermic membrane. During the sixth week, after the cavity of the pharynx has appeared; the membrane gives way in front, forming a large opening, which may be called the first opening of the mouth. At this time, however, the face is entirely open in front as far back as the ears. The first, or the superior visceral arch, now appears as a projection of the middle blastodermic layer, extending forward. This is soon marked by two secondary projections, the upper projection forming the superior maxillary portion of the face, and the lower, the inferior maxilla. The two projections which form the lower jaw soon meet in the median line, and their superior margin is the lower lip. At the same time there is a projection from above, extending between the two superior projections, which is called the frontal, or intermaxillary process. This extends from the forehead (that portion which covers the front of the cerebrum) downward. The superior maxillary projections then advance forward, gradually passing to meet the frontal process, but leaving two small openings on either side of the median line, which are the openings of the nostrils. The upper portion of the frontal process thus forms the nose; but below, is the lower end of this process, which is at first split in the median line, projects below the nose, and forms the incisor process, at the lower border of which are finally developed the incisor teeth. As the superior maxillary processes advance forward, the eyes are moved, as it were, from the sides of the head and present anteriorly, until finally their axes become parallel. These processes advance from the two sides, come to the sides of the incisor process beneath the nose, unite with the incisor process on either side, and their lower margin, with the lower margin of the incisor process, forms the upper lip; but, before this, the two lateral halves of the incisor process have united in the median line. At the bottom of the cavity of the mouth, a small papilla makes its appearance, which gradually elongates and forms the tongue.

While this process of development of the anterior portion of the first visceral arch is going on, at its posterior portion, we have developing, the malleus and incus, the former being at first connected with the cartilage of Meckel, which extends along the inner surface of the inferior maxilla, the cartilages from either side meeting at the chin. The cleft between the first and the second visceral arch has closed, except at its posterior portion, where an opening is left for the external auditory meatus, the cavity of the tympanum, and the Eustachian tube.

At the same time, the second visceral arch advances and forms the stapes, the styloid ligament, and the lesser cornua of the hyoid bone. The third arch advances in the same way; and the arches from the two sides meet, become united in the median line, and form the body and the greater cornua of the hyoid. The clefts between the second and the third and between the third and fourth arches become obliterated by the deposition of plastic matter.

The fourth arch forms the sides of the neck and the larynx, the arytenoid cartilages being developed first. In front of the larynx and just behind the tongue, is a little elevation, which is developed into the epiglottis. The openings of the nostrils appear during the second half of the second month. A little elevation, the nose, appears between these openings, and the nasal cavity begins to be separated from the mouth. The lips are distinct during the third month, and the tongue first appears in the course of the seventh week.

FIG. 303.—*Mouth of a human embryon of from twenty-five to twenty-eight days; magnified 15 diameters.* (Coste.)

1, median or frontal process, the inferior portion of which is considerably enlarged; 2, right nostril; 3, left nostril; 4, 4, inferior maxillary processes, already united in the median line; 5, 5, superior maxillary processes, which have become quite prominent and have descended to the level of the slope of the frontal process; 6, mouth; 7, first visceral arch; 8, second visceral arch; 9, third visceral arch; 10, eye; 11, ear.

The above sketch of the mode of development of the face enables us to understand the origin of certain of the more common malformations of this part. When, by an arrest of development, the superior maxilla on one side fails to unite with the side of the incisor process, we have the very common deformity known as single hare-lip. If this union fail on both sides, we have double hare-lip, when the incisor process is usually more or less projecting. As a very rare deformity, it is sometimes observed that the two sides of the incisor process have failed to unite with each other, leaving a fissure in the median line.

It is somewhat difficult to comprehend the exact mode of development of the face by verbal description alone; but it will be readily understood, after the account we have just given, by studying Figs. 303, 304, and 305, copied from the great atlas of Coste, and plates I. and II., Figs. A, B, C, and D, facing page 920.

The palatine arch is developed by two processes, which arise on either side from the incisor process, pass backward and upward, and finally meet and unite in the median line. The union of these forms the plane of separation between the mouth and the nares; and want of fusion of these processes, from arrest of development, produces the malformation known as cleft palate, in which the fissure is always in the median line. At the same time, a vertical process forms in the median line, between the palatine arch and the roof of the nasal cavity, which separates the two nares.

Development of the Teeth.—Recent embryological researches have shown that the old idea of the development of the dental papillæ in the bottom of a gutter formed at the border of either jaw is erroneous. According to the most recent observers, the first appearance of the organs for the development of the teeth is marked by the formation of a cellular projection extending the entire length of the rounded border of each jaw, which forms a rounded band above and dips down somewhat into the subjacent structure. This band is readily separated by maceration, and the removal of the portion that dips into the maxilla leaves a groove, which is thought to be the explanation of the description of a groove by the earlier writers. This band extends the entire length of the jaws without interruption. Its superior surface is rounded, and that portion which dips into the subjacent mucous structure is wedge-shaped, so that its section has the form of a V.

As soon as this primitive band is formed, which occurs at the sixth or seventh week, a flat band projects from its internal surface, near the mucous structure, which is called the epithelial band. This also extends over the entire length of the jaws. It is thin, flattened, with its free edge curved inward and toward the jaw, and is composed, at first, of a central layer of polygonal cells, covered by a layer of columnar epithelium.

At certain points—these points corresponding to the situation of the true dental bulbs—there appear rounded enlargements at the free margin of the epithelial band just described. Each one of these is developed into one of the structures of the perfect tooth. The mechanism of the formation of this, which is called the enamel-organ, and of the dental bulb is as follows:

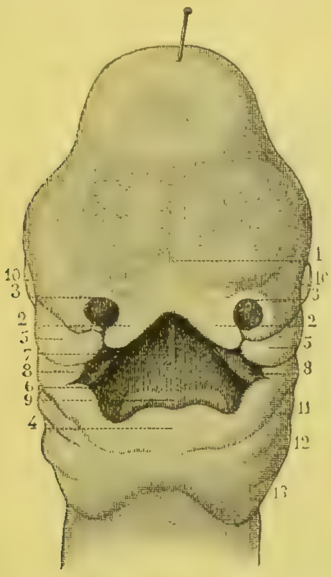


FIG. 304.—*Mouth of a human embryon of thirty-five days.* (Coste.)

1, frontal process widely sloped at its inferior portion; 2, 2, incisor processes produced by this sloping; 3, 3, nostrils; 4, lower lip and maxilla, formed by the union of the inferior maxillary processes; 5, 5, superior maxillary processes contiguous to the incisor process; 6, mouth, still confounded with the nasal fossæ; 7, first appearance of the closure of the nasal fossæ; 8, 8, first appearance of the two halves of the palatine arch; 9, tongue; 10, 10, eyes; 11, 12, 13, visceral arches.

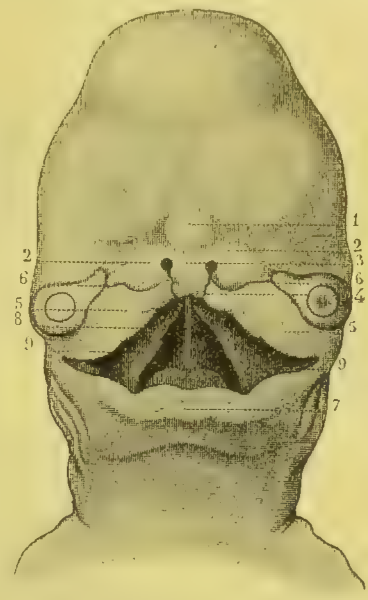


FIG. 305.—*Mouth of an embryon of forty days.* (Coste.)

1, first appearance of the nose; 2, 2, first appearance of the alæ of the nose; 3, appearance of the closure beneath the nose; 4, middle, or median portion of the upper lip, formed by the approach and union of the two incisor processes, a little notch in the median line still indicating the primitive separation of the two processes; 5, 5, superior maxillary processes, forming the lateral portions of the upper lip; 6, 6, groove for the development of the lachrymal sac and the nasal canal; 7, lower lip; 8, mouth; 9, 9, the two lateral halves of the palatine arch, already nearly approximated to each other in front, but still widely separated behind.

A rounded enlargement appears at the margin of the epithelial band. This soon becomes directed downward (adapting our description to the lower jaw) and dips into the mucous structure, being at first connected with the epithelial band by a narrow pedicle, which soon disappears, leaving the enlargement enclosed completely in a follicle. This is the dental follicle, and it has no connection with the wedge-shaped band which we described first. While this process is going on, a conical bulb appears at the bottom of the follicle. The enamel-organ, formed from the epithelial band, becomes excavated or cup-shaped at its under surface and fits over the dental bulb, becoming united to it.

The tooth, at this time, consists of the dental bulb, with the enamel-organ closely fitted to its projecting surface. The enamel-organ is developed into the enamel; the dental bulb, which is provided with vessels and nerves, becomes the tooth-pulp; and, upon the surface of the dental bulb, the dentine, or ivory, is developed in successive layers. The cement is developed by successive layers upon that portion of the dentine which forms the root of the tooth. As these processes go on, the tooth projects more and more, the upper part of the wall of the follicle gives way, and the tooth finally appears at the surface.

[1] The periods of development indicated for these diagrams are somewhat earlier than those which we have noted in the text; but it is impossible to fix these with absolute accuracy, and all the estimates given by authors are understood to be merely approximative.

The permanent teeth are developed beneath the follicles of the temporary, or milk-teeth. The first appearance is a prolongation or diverticulum from the enamel-organ of the temporary tooth, which dips more deeply into the mucous structure. This becomes the enamel-organ of the permanent tooth; and the successive stages of development of the dental follicles and the dental pulp progress in the same way as in the temporary teeth. As the permanent teeth increase in size, they gradually encroach upon the roots of the temporary teeth. The roots of the latter are absorbed, the permanent teeth ad-

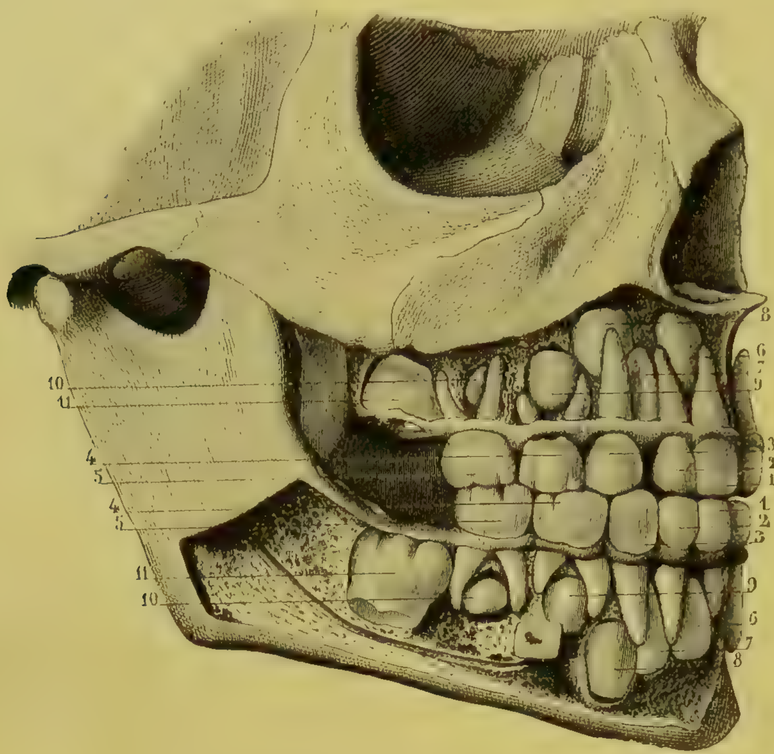


FIG. 306.—*Temporary and permanent teeth.* (Sappey.)
1, 1, temporary central incisors; 2, 2, temporary lateral incisors; 3, 3, temporary canines: 4, 4, temporary anterior molars; 5, 5, temporary posterior molars; 6, 6, permanent central incisors; 7, 7, permanent lateral incisors; 8, 8, permanent canines; 9, 9, permanent first bicuspids; 10, 10, permanent second bicuspids; 11, 11, first molars.

vance more and more toward the surface, and the crown of each temporary tooth is finally pushed out. The number of the temporary teeth is twenty, while there are thirty-two permanent teeth. Thus there are three permanent teeth on either side of both jaws, which are developed *de novo* and are not preceded by temporary structures.

The first dental follicles usually appear in regular succession. The follicles for the internal incisors of the lower jaw appear first, this occurring at about the ninth week. All of the follicles for the temporary teeth are completely formed at about the eleventh or the twelfth week.

The temporary teeth appear successively, the corresponding teeth appearing a little earlier in the lower jaw. The usual order, subject to certain exceptional variations, according to Sappey, is as follows:

The four central incisors appear from six to eight months after birth.
The four lateral incisors appear from seven to twelve months after birth.
The four anterior molars appear from twelve to eighteen months after birth.
The four canines appear from sixteen to twenty-four months after birth.
The four posterior molars appear from twenty-four to thirty-six months after birth.

The order of eruption of the permanent teeth is as follows:

The two central incisors of the lower jaw appear from the sixth to the eighth year.
The two central incisors of the upper jaw appear from the seventh to the eighth year.
The four lateral incisors appear from the eighth to the ninth year.
The four first bicuspids appear from the ninth to the tenth year.
The four canines appear from the tenth to the eleventh year.
The four second bicuspids appear from the twelfth to the thirteenth year.

The above are the permanent teeth which replace the temporary teeth. The permanent teeth which are developed *de novo* appear as follows:

The first molars appear from the sixth to the seventh year.
The second molars appear from the twelfth to the thirteenth year.
The third molars appear from the seventeenth to the twenty-first year.

Development of the Genito-Urinary System.

The genital and the urinary organs are developed together and are both preceded by the appearance of two large, symmetrical structures, known as the Wolffian bodies, or the bodies of Oken. These are sometimes called the false or the primordial kidneys. They appear at about the thirtieth day, develop very rapidly on either side of the spinal column, and are so large as to almost fill the cavity of the abdomen. Fig. 307, representing a specimen in the possession of Prof. Dalton, shows how large these bodies are in the early life of the embryon, at which time their function is undoubtedly very important.

Very soon after the Wolffian bodies have made their appearance, we can distinguish, at their inner borders, two ovoid bodies, which are finally developed into the testicles, for the male, or the ovaries, for the female. At their external borders, are two ducts, on either side, one of which, the internal, is called the duct of the Wolffian body. This finally disappears, in the female, but it is developed into the vas deferens, in the male. The other duct, which is external to the duct of the Wolffian body, disappears, in the male, but it becomes the Fallopian tube, in the female. This is known as the duct of Müller. Behind the Wolffian bodies, are developed the kidneys and the suprarenal capsules.

Fig. 307.—*Fœtal pig, ⅝ of an inch long.* From a specimen in the possession of Prof. Dalton.
1, heart; 2, anterior extremity; 3, posterior extremity; 4, Wolffian body. The abdominal walls have been cut away, in order to show the position of the Wolffian bodies.

As the development of the Wolffian bodies attains its maximum, their structure becomes somewhat complex. From their proper ducts, which are applied directly to their outer borders, tubes make their appearance at right angles to the ducts, which extend into the substance of the bodies and become somewhat convoluted at their extremities. These tubes communicate directly with the ducts, and the ducts themselves open into the lower part of the intestinal canal, opposite to the point of its communication with the allantois. The tubes of the Wolffian bodies are simple, terminating in single, somewhat dilated, blind extremities, are lined with epithelium, and are penetrated, at their extremities, by blood-vessels, which form coils or convolutions in their interior. These are undoubtedly organs of depuration for the embryon and take on the function to be subsequently assumed by the kidneys; but, in the female, they are temporary structures, disappearing as development advances, and having nothing to do with the development of the true urinary organs.

The testicles or ovaries are developed at the internal and anterior surface of the Wolffian bodies, first appearing in the form of small, ovoid masses. Beginning just above and passing along the external borders of the Wolffian bodies, are the tubes called the ducts of Müller. These at first open into the intestine, near the point of entrance of the

Wolffian ducts. In the female, their upper extremities remain free, except the single fimbria which is connected with the ovary. Their inferior extremities unite with each other, and, at their point of union, they form the uterus. When this union is incomplete, we have the malformation known as double uterus, which may be associated with a double vagina. The Wolffian bodies and their ducts disappear, in the female, at about the fiftieth day. A portion of their structure, however, persists, in the form of a collection of closed tubes, constituting the parovarium, or organ of Rosenmüller.

In the female, the ovaries pass down no farther than the pelvic cavity; but the testicles, which are at first in the abdomen of the male, finally descend into the scrotum. As the testicles descend, they carry with them the Wolffian duct, that portion of the Wolffian body which is permanent constituting the head of the epididymis. At the same time, a cord appears, attached to the lower extremity of the testicle and extending to the symphysis pubis. This is called the gubernaculum testis. It is at first muscular, but the muscular fibres disappear during the later periods of utero-gestation. It is not known that its muscular structure takes any part, by contractile action, in the descent of the testicle in the human subject. The epididymis and the vas deferens are formed from the Wolffian body and the Wolffian duct.

At about the end of the seventh month, the testicle has reached the internal abdominal ring; and, at this time, a double tubular process of peritoneum, covered with a few fibres from the lower portion of the internal oblique muscle of the abdomen, gradually extends into the scrotum. The testicle descends, following this process of peritoneum, which latter becomes eventually the visceral and parietal portion of the tunica vaginalis. The canal of communication between the abdominal cavity and the cavity of the scrotum is finally closed, and the tunica vaginalis is separated from the peritoneum. The fibres derived from the internal oblique constitute the cremaster muscle.

At the eighth or the ninth month, the testicles have reached the external abdominal ring and then soon descend into the scrotum. The vas deferens, as we have seen, passes from the testicle, along the base of the bladder, to open into the prostatic portion of the urethra; and, as development advances, two sacculated diverticula from these tubes make their appearance, which are attached to the bladder and constitute the vesiculæ seminales.

As the ovaries descend to their permanent situation in the pelvic cavity, there appears, attached to the inner extremity of each, a rounded cord, analogous to the gubernaculum testis. A portion of this, connecting the ovary with the uterus, constitutes the ligament of the ovary; and the inferior portion forms the round ligament of the uterus, which passes through the inguinal canal and is attached to the symphysis pubis.

The development of the external organs of generation will be studied after we have described the development of the urinary apparatus.

Development of the Urinary Apparatus.—Behind the Wolffian bodies, and developed entirely independently of them, the kidneys, suprarenal capsules, and ureters make their appearance. The kidneys are developed in the form of little, rounded bodies, composed of short, blind tubes, all converging toward a single point, which is the hilum. These tubes increase in length, branch, become convoluted in a certain portion of their extent, and finally assume the structure and arrangement of the renal tubules, with their Malpighian bodies, blood-vessels, etc. They all open into the hilum. At the same time that the kidneys are undergoing development, the suprarenal capsules are formed at their superior extremities. These bodies, the function of which is unknown, are relatively so much larger in the fœtus than in the adult, that they have been supposed to be peculiarly important in intra-uterine life, though nothing definite is known upon this point. The kidneys are relatively very large in the fœtus. Their proportion to the weight of the body, in the fœtus, is 1 to 80, and, in the adult, 1 to 240. The ureters are undoubtedly developed as tubular processes from the kidneys, which finally extend to open into the bladder. This fact is shown by certain cases of malformation, in which the ureters have not reached the bladder, but terminate in blind extremities. The development of the

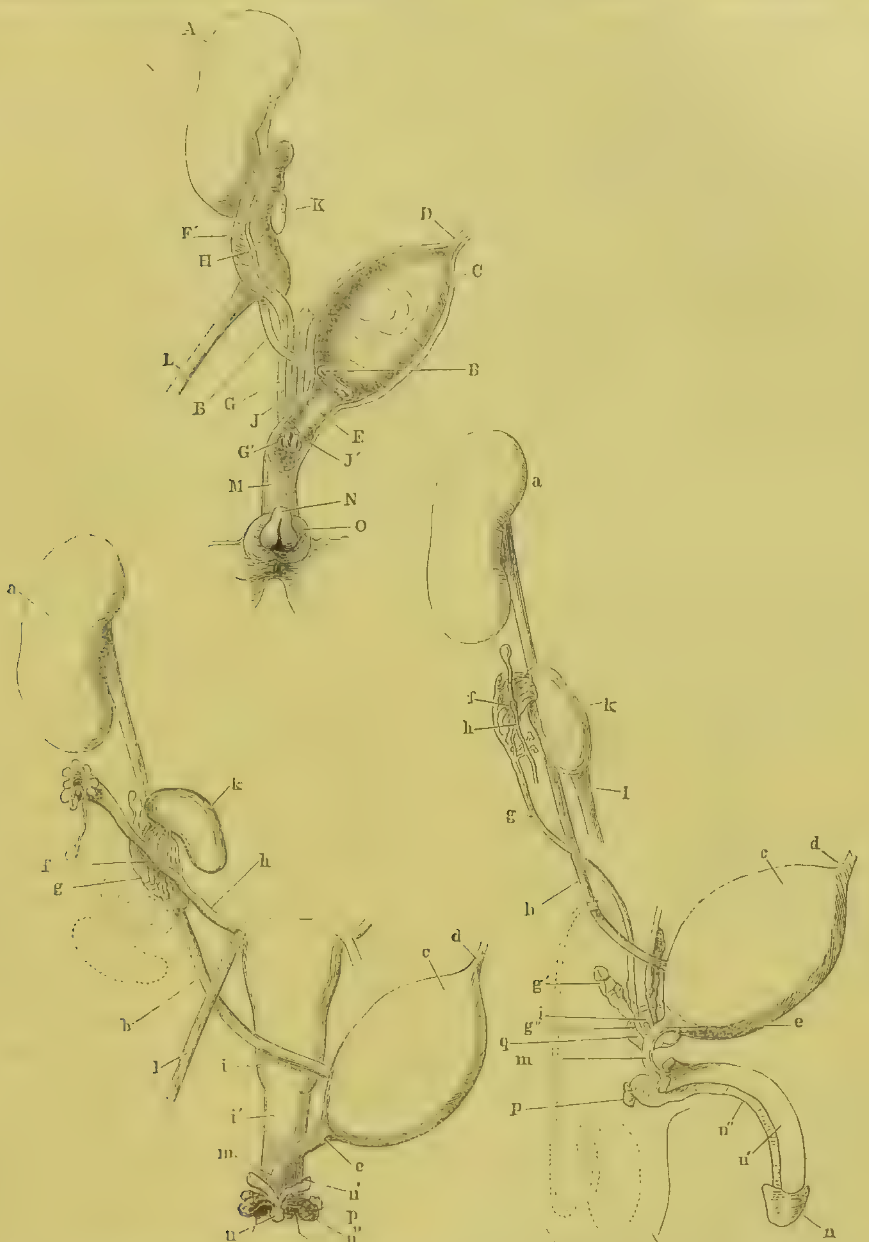


Fig. 308.—*Diagrammatic representation of the genito-urinary system.* (Henle.)

A, embryonic condition, in which there is no distinction of sex; B, female form; C, male form. The dotted lines in B and C represent the situations which the male and female genital organs assume after the descent of the ovaries and testicles. The small letters in B and C correspond to the capital letters in A.

Fig. 308 A.—A, kidney; B, ureter; C, bladder; D, urachus, developed into the median ligament of the bladder; E, constriction which becomes the urethra; F′, Wolffian body; G, Wolffian duct, with its opening below, G′; H, duct of Müller, united below, from the two sides, into a single tube, J, which presents a single opening, J′, between the openings of the Wolffian ducts; K, ovary or testicle; L, gubernaculum testis or round ligament of the uterus; M, genito-urinary sinus; N, O, external genitalia.

Fig. 308, B (female).—a, kidney; b, ureter; c, bladder; d, urachus; e, urethra; f, remains of the Wolffian body (parovarium); g, remnant of the Wolffian duct; h, Fallopian tube; i, uterus; i′, vagina; k, ovary; l, round ligament of the uterus; m, extremity of the urethra; n, clitoris; n′ corpus cavernosum of the clitoris; n″, bulb of the vestibule; o, external genital opening; p, excretory duct of the gland of Bartholinus.

Fig. 308, C (male).—a, kidney; b, ureter; c, bladder; d, urachus; e, m, urethra; f, epididymis; g, vas deferens; g′, seminal vesicle; g″, ejaculatory duct; h, i, remains of the duct of Müller; k, testicle; l, gubernaculum testis; n, n′, n″. urethra and penis; o, scrotum; p, gland of Cowper; q, prostate.

genito-urinary system can be readily understood, after the description we have just given, by a study of Fig. 308.

External Organs of Generation.—The external organs of generation begin to be developed at about the fifth week. At the inferior extremity of the body of the embryon, a small, ovoid eminence appears in the median line, at the lower portion of which there is a longitudinal slit, which forms the common opening of the anus and the genital and urinary passages. This is the cloaca. There is soon developed, internally, a septum, which separates the rectum from the vagina, the urethra of the female opening above. In the male, this septum is developed between the rectum and the urethra, the generative and the urinary passages opening together. From this median prominence, two lateral, rounded bodies make their appearance. These are developed, with the median elevation, into the glans penis and corpora cavernosa of the male, or into the clitoris and the labia minora of the female. In the male, these two lateral prominences unite in the median line and enclose the spongy portion of the urethra. When there is a want of union in the cavernous bodies in the male, we have the malformation known as hypospadias. In the female, there is no union in the median line, and an opening remains between the two labia minora. The scrotum in the male is analogous to the labia majora of the female; the distinction being that the two sides of the scrotum unite in the median line, while the labia majora remain permanently separated. This analogy is farther illustrated by the anatomy of inguinal hernia, in which the intestine descends into the labia, in the female, and into the scrotum, in the male. It sometimes occurs, also, that the ovaries descend, very much as the testicles pass down in the male, and pass through the external abdominal ring.

From the above description, it is easy to imagine how malformation and malposition of the genital organs may occur, so that it is difficult to determine the sex of the individual. We may have, in a male, absence of beard and a certain degree of development of the mammary glands, with a pelvic conformation approximating, more or less, that of the female; and, on the other hand, a female may have a beard, slight mammary development, and a general conformation of the body resembling that of a male. This may be associated with corresponding malformations of the genital organs. We may, for example, have a large development of the clitoris, descent of the ovaries, more or less complete occlusion of the vagina, and union of the labia majora, so that it is difficult to determine the sex from an external examination; and opposite vices of formation may occur in the male, the testicles remaining in the pelvic cavity. It is not surprising, therefore, that beings have existed of undetermined sex, and many cases of this kind are on record. Two cases have been reported in which, apparently, the two sexes were combined. The first case was presented to the Medical Society of Vienna, by Rokitansky, in 1869. This case presented, on post-mortem examination, two ovaries with their Fallopian tubes, a rudimentary uterus, a testicle, and a vas deferens containing spermatozoids. This individual menstruated, had an imperfect penis, and a bifid scrotum. The sexual indifference was absolute. The second case was published by Heppner, in 1872. This was a child, six weeks old, which had been preserved in alcohol for several years. It presented ovaries, Fallopian tubes, a uterus, and a vagina opening into the urethra. There were also two bodies which were shown, upon microscopical examination, to be testicles, a penis with hypospadia, and a prostate; but there were neither vesiculæ seminales nor vasa deferentia.

Development of the Circulatory System.

The blood and the blood-vessels are developed very early in the life of the ovum and make their appearance nearly as soon as the primitive trace. The mode of development of the first vessels differs from that of vessels formed later, as they appear *de novo* in the blastodermic layers, while afterward, vessels are formed as prolongations of preëxisting tubes. Soon after the external and the internal blastodermic membranes have become separated from each other, and the intermediate membrane has been formed at the thickened portion of the ovum which is destined to be developed into the embryon, certain of the blastodermic cells undergo a transformation into blood-corpuscles. These are larger than the blood-corpuscles of the adult and are generally nucleated. At about the same time (it may be before or after the appearance of the corpuscles, for this point is undetermined) certain of the blastodermic cells fuse with each other and arrange themselves so as to form vessels. Leucocytes are probably developed in the same way as the red corpuscles. The vessels thus formed constitute the area vasculosa, which is the beginning of what is known as the first circulation.

It is evident that the relations of the embryon at different stages of development must require certain variations in the arrangement of the circulatory system. The ovum has, of course, no vascular connection with the mother before the formation of the allantois. It has undergone, however, a certain degree of development, and presents a circulatory system, which extends over the umbilical vesicle. This stage of development of the vascular system constitutes what is known as the first circulation. As the allantois is developed, the circulation over the umbilical vesicle becomes unimportant, and its vessels disappear. Vessels then extend into the allantois, are finally developed into the fœtal portion of the placenta, and what is known as the second circulation is established. This circulation continues throughout intra-uterine life, and, as we know, the embryon and fœtus depend entirely upon the placenta for materials for respiration, nutrition, and growth. At birth, the requirements are again changed. The placental circulation is then abolished, and the arrangement of vessels peculiar to it disappears. Now, for the first time, the pulmonary circulation becomes important. All the blood passes through the lungs before it is sent to the general system, the two sides of the heart become completely separated from each other, and the third, the pulmonary, or adult circulation, is established.

The First, or Vitelline Circulation.—In the development of oviparous animals, the first, or vitelline circulation is very important; for, by these vessels, the contents of the nutritive yolk are taken up and carried to the embryon, constituting the only source of material for its nutrition and growth. In mammals, however, nutritive matter is absorbed almost exclusively from the mother, by simple endosmosis, before the placental circulation is established, and by the placental vessels, at a later period. The vitelline circulation is therefore not important, and the vessels disappear with the atrophy of the umbilical vesicle.

The area vasculosa, in mammals, consists of vessels coming from the body of the embryon, forming a nearly circular plexus in the substance of the vitellus, around the embryon. The vessels of this plexus open into a sinus at the border of the area, called the sinus terminalis. It is probable that these vessels are developed *de novo* in the intermediate blastodermic layer and are not preceded by a distinct membrane; but such a membrane has been described under the name of the vascular blastodermic layer.

If we examine the ovum when the area vasculosa is first formed, we see the embryon lying in the direction of the diameter of the nearly circular plexus of blood-vessels. The plexus surrounds the embryon, except at the cephalic extremity, where the terminal sinuses of the two sides curve downward toward the head, to empty into the omphalo-mesenteric veins. As the umbilical vesicle is separated from the body of the embryon, it carries the plexus of vessels of the area vasculosa with it, the vessels of communication with the embryon being the omphalo-mesenteric arteries and veins. As these processes are going on, the great central vessel of the embryon becomes enlarged and twisted upon itself, at a point just below the cephalic enlargement of the embryon, between the inferior extremity of the pharynx and the superior *cul-de-sac* of the intestinal canal. The excavation which receives this vessel is called the fovea cardiaca. The different stages of development of the heart, which is formed of the twisted portion of the central vessel, will be described farther on. Simple, undulatory movements take place in the heart of the chick at about the middle of the second day; but there is not, at that time, any regular circulation. At the end of the second day or the beginning of the third, the currents of the circulation are established. The time of the first appearance of the circulation in the human embryon has not been accurately determined.

FIG. 309.—*Area vasculosa.* (Bischoff.)
a, *a*, *b*, sinus terminalis; *c*, omphalo-mesenteric vein; *d*, heart; *e*. *f*, *f*, posterior vertebral arteries.

In the arrangement of the vessels for the first circulation of the embryon, the heart is situated exactly in the median line and gives off two arches which curve to either side and unite into a single central trunk at the spinal column below. These are the two aortæ, and the single trunk formed by their union becomes the abdominal aorta. The two aortic arches, one of which only is permanent, are sometimes called the inferior vertebral arteries. These vessels give off numerous branches, which pass into the area vasculosa. Two of these branches, however, are larger than the others, pass to the umbilical vesicle, and are called the omphalo-mesenteric arteries. In the embryon of mammals, there are, at first, four omphalo-mesenteric veins, two superior, which are the larger, and two inferior; but, as development advances, the two inferior veins are closed, and we then have two omphalo-mesenteric arteries and two omphalo-mesenteric veins. At about the fortieth day, one artery and one vein disappear, and we have then but one omphalo-mesenteric artery and one vein. Soon after, as the circulation becomes established in the allantois, the vessels of the umbilical vesicle and the omphalo-mesenteric vessels are obliterated, and the first circulation is superseded by the second.

As the septum between the two ventricles makes its appearance, that division of the right aortic arch which constitutes the vascular portion of one of the branchial arches disappears and loses its connection with the abdominal aorta; a branch, however, persists during the whole of intra-uterine life and constitutes the ductus arteriosus, and another branch is permanent, forming the pulmonary artery.

The Second, or Placental Circulation.—As the omphalo-mesenteric vessels disappear, and as the allantois is developed to form the chorion, two vessels (the hypogastric arteries) are given off, first from the abdominal aorta; but afterward, as the vessels going to the lower extremities are developed, the branching of the abdominal aorta is such that the vessels become connected with the internal iliac arteries. The hypogastric arteries pass to the chorion through the umbilical cord and constitute the two umbilical arteries. At first, there are two umbilical veins; but one of them afterward disappears, and there is finally but one vein in the umbilical cord. It is in this way—the umbilical arteries carrying the blood to the tufts of the fœtal placenta, which is returned by the umbilical vein—that the placental circulation is established.

Corresponding to the four visceral arches, which we have described in connection with the development of the face, are four vascular arches. One of these disappears, and the remaining three undergo certain changes, by which they are converted into the vessels going to the head and the superior extremities. The anterior arches on the two sides are converted into the carotids and subclavians; the second, on the left side, is converted into the permanent aorta, and the right is obliterated; the third, on either side, is converted into the right and left pulmonary arteries. In the early stages of the development of the vascular system of mammals, the conditions have been compared to the permanent arrangement of the circulatory system in fishes. The heart of fishes remains single; and the heart of mammals is at first single, but afterward it becomes divided by the development of the intra-ventricular septum. The branchial arches in fishes are permanent, they receive all the blood from the aortic bulb, and the blood from these arches then passes into the dorsal aorta. This is very nearly the condition of the vascular system when the branchial arches first appear in the embryon of mammals.

Fig. 310.—*Transformation of the system of aortic arches into permanent arterial trunks in the mammalia.* (Von Baer.)
B, aortic bulb: 1, 2, 3, 4, 5, on either side, the five pairs of aortic arches; 5, 5, the earliest in their appearance; 1, 1, the most recent; *c, c*, the two carotids, still united, which are separated at a later period; *s, s*, the two subclavians, the right arising from the arteria innominata; *a, a*, the aorta; *p, p*, the pulmonary arteries; *ca*, the ductus arteirosus; *cd*, the left artieral canal, which is finally obliterated.

The changes of the branchial arches which we have described are illustrated in the diagrammatic Fig. 310. In this figure, the three branchial arches that remain and participate in the development of the upper portion of the vascular system are 1, 2, 3, on either side. The two anterior (3, 3) become the carotids (*c, c*) and the subclavians (*s, s*). The second (2, 2) is obliterated on the right side, and becomes the arch of the aorta on the left side. The third (1, 1), counting from above downward, is converted into the pulmonary arteries of the two sides. Upon the left side, there is a large anastomosing vessel (*ca*), between the pulmonary artery of that side and the arch of the aorta, which is the ductus arteriosus. The anastomosing vessel (*cd*) between the right pulmonary artery and the aorta, is obliterated.

The mode of development of the veins is very simple. Two venous trunks make their appearance by the sides of the spinal column, which are called the cardinal veins, and run parallel with the superior vertebral arteries, or the two aortæ, emptying finally into the auricular portion of the heart by two canals, which are called the canals of Cuvier. These veins change their relations and connections as the first circulation is replaced by the second. The omphalo-mesenteric vein opens into the heart between the two canals of Cuvier. As development advances, the liver is formed in the course of this vessel, a short distance below the heart, and the vein ramifies in its substance; so that the blood of the omphalo-mesenteric vein passes through the liver before it gets to the heart. We have seen that the omphalo-mesenteric vein is obliterated as the umbilical vein makes its appearance. The blood from the umbilical vein is at first emptied directly into the heart; but this vessel soon establishes the same relations with the liver as the omphalo-mesenteric vein, and its blood passes through the liver before it reaches the central organ of the circulation. As the omphalo-mesenteric vein atrophies, the mesenteric vein, bringing the blood from the intestinal canal, is developed, and this penetrates the liver, becoming, finally, the portal vein.

As the lower extremities are developed, the inferior vena cava makes its appearance between the two inferior cardinal veins. This vessel receives an anastomosing branch from the umbilical vein, before it penetrates the liver, and this branch is the ductus venosus. As the inferior vena cava increases in size, it communicates below with the two inferior cardinal veins; and that portion of the two inferior cardinal veins which remains constitutes the two iliac veins. The inferior cardinal veins, between that portion which forms the iliac veins and the heart, finally become the right and the left azygos veins.

The right canal of Cuvier, as the upper extremities are developed, enlarges and becomes the vena cava descendens, receiving, finally, all the blood from the head and the superior extremities. The left canal of Cuvier undergoes atrophy and finally disappears. The upper portion of the superior cardinal veins is developed into the jugulars and subclavians on the two sides. As the lower portion of the left cardinal vein and the left canal of Cuvier atrophy, a venous trunk appears, connecting the left subclavian with the right canal of Cuvier. This increases in size and becomes the left vena innominata, which connects the left subclavian and internal jugular with the vena cava descendens.

Development of the Heart.—The central enlargement of the vascular system in the first circulation, which becomes the heart, is twisted upon itself by a single turn. The portion connected with the cephalic extremity of the embryon gives origin to the arterial system, and the portion connected with the caudal extremity receives the blood from the venous system. The walls of the arterial portion of the heart soon become thickened, while the walls of the venous portion remain comparatively thin. There then appears a constriction, which partly separates the auricular from the ventricular portion. At a certain period of development, the heart presents a single auricle and a single ventricle.

The division of the heart into two ventricles appears before the two auricles are separated. This is effected by a septum, which gradually extends from the apex of the heart upward toward the auricular portion. At the seventh week, there is a large opening between the two ventricles. This gradually closes from below upward, the heart becomes more pointed, and the separation of the two ventricles is complete at about the end of the second month.

At about the end of the second month, a septum begins to be formed between the auricles. This extends from the base of the heart toward the ventricles, but it leaves an opening between the two sides (the foramen ovale, or the foramen of Botal) which persists during the whole of fœtal life. At the anterior edge of the opening of the vena cava ascendens into the right auricle, there is a membranous fold, which projects into the auricle. This is the valve of Eustachius, and it divides the right auricle incompletely into two portions.

During the sixth week, the heart is vertical and situated in the median line, with the aorta arising from the centre of its base. At the end of the second month, it is raised up by the development of the liver, and its point presents forward. During the fourth month, it is twisted slightly upon its axis, and the point presents to the left. At this time, the auricular portion is larger than the ventricles; but the auricles diminish in their relative capacity during the latter half of intra-uterine life. The pericardium makes its appearance during the ninth week.

Early in intra-uterine life, the relative size of the heart is very great. At the second month, its weight, in proportion to the weight of the body, is 1 to 50. This proportion, however, gradually diminishes until, at birth, the ratio is 1 to 120. The proportionate weight in the adult is about 1 to 160. During about the first half of intra-uterine life, the thickness of the two ventricles is nearly the same; but, after that time, the relative thickness of the left ventricle gradually increases.

Peculiarities of the Fœtal Circulation.—In studying the complete course of the blood in the fœtus, which constitutes the second, or the placental circulation, we note peculiarities in two portions of the circulatory system. In the one, a peculiar arrangement is necessitated by the passage of blood to and from the placenta; and in the other, the character of the blood coming from the placenta necessitates a peculiar arrangement of the heart and the great vessels.

The branches from the internal iliac arteries, which pass to the fœtal tufts of the placenta, do not exist in the adult. The ductus venosus, which conveys a portion of the blood of the umbilical vein to the vena cava ascendens, and the umbilical vein itself do not exist in the adult.

The Eustachian valve, situated at the inner margin of the vena cava ascendens as it opens into the right auricle, does not exist in the adult. The foramen ovale, or the opening between the right and the left auricle, through which the blood from the vena cava ascendens is directed into the left auricle, does not exist in the adult. The ductus arteriosus, which conveys the blood from the left pulmonary artery to the arch of the aorta, does not exist in the adult. In the adult, the pulmonary arteries receive all the blood from the right ventricle. In the fœtus, the pulmonary arteries receive a small quantity of blood, as compared with that which passes to the aorta through the ductus arteriosus. Keeping in view these peculiarities of the circulatory apparatus, the entire course of the blood, during fœtal life, is as follows:

Beginning with the abdominal aorta, we follow the course of blood into the two primitive iliacs, and thence into the internal iliacs. From the two internal iliacs, the two hypogastric arteries arise, which ascend along the sides of the bladder to its fundus, thence pass to the umbilicus and go to the placenta, forming the two umbilical arteries. In this way, the blood of the fœtus goes to the placenta.

The umbilical vein enters the body of the fœtus at the umbilicus; it passes along the margin of the suspensory ligament to the under surface of the liver; it gives off one branch of large size, and one or two smaller branches to the left lobe; it sends a branch each to the lobus quadratus and the lobus Spigelii; and the vessel reaches the transverse fissure. At the transverse fissure, it divides into two branches, the larger of which joins the portal vein and enters the liver; and the smaller, which is the ductus venosus, passes to the vena cava ascendens, at the point where it receives the left hepatic vein. Thus, the greater part of the blood returned to the fœtus from the placenta passes through the liver, a relatively small quantity being emptied into the vena cava by the ductus venosus.

The vena cava ascendens, containing the placental blood which has passed through the liver, the blood conveyed directly from the umbilical vein by the ductus venosus, and the blood from the lower extremities, passes to the right auricle. As the blood enters the right auricle, it is directed by the Eustachian valve, passing behind the valve, through the foramen ovale, into the left auricle. At the same time, the blood from the head and the superior extremities passes down, by the vena cava descendens, in front of the Eustachian valve, through the right auricle, into the right ventricle. The arrangement of the Eustachian valve is such, that the right auricle simply affords a passage for the two currents of blood; the one, from the vena cava ascendens, through the foramen ovale, passes into the left auricle and the left ventricle; and the other, from the vena cava descendens, passes through the right auriculo-ventricular opening, into the right ventricle. It is probable, indeed, that there is very little admixture of these two currents of blood in the natural course of the fœtal circulation. Reid injected the vena cava ascendens with red, and the vena cava descendens with yellow, in a fœtus of seven months, and he found very little mixture of the two colors in the passage of the injected material through the right auricle.

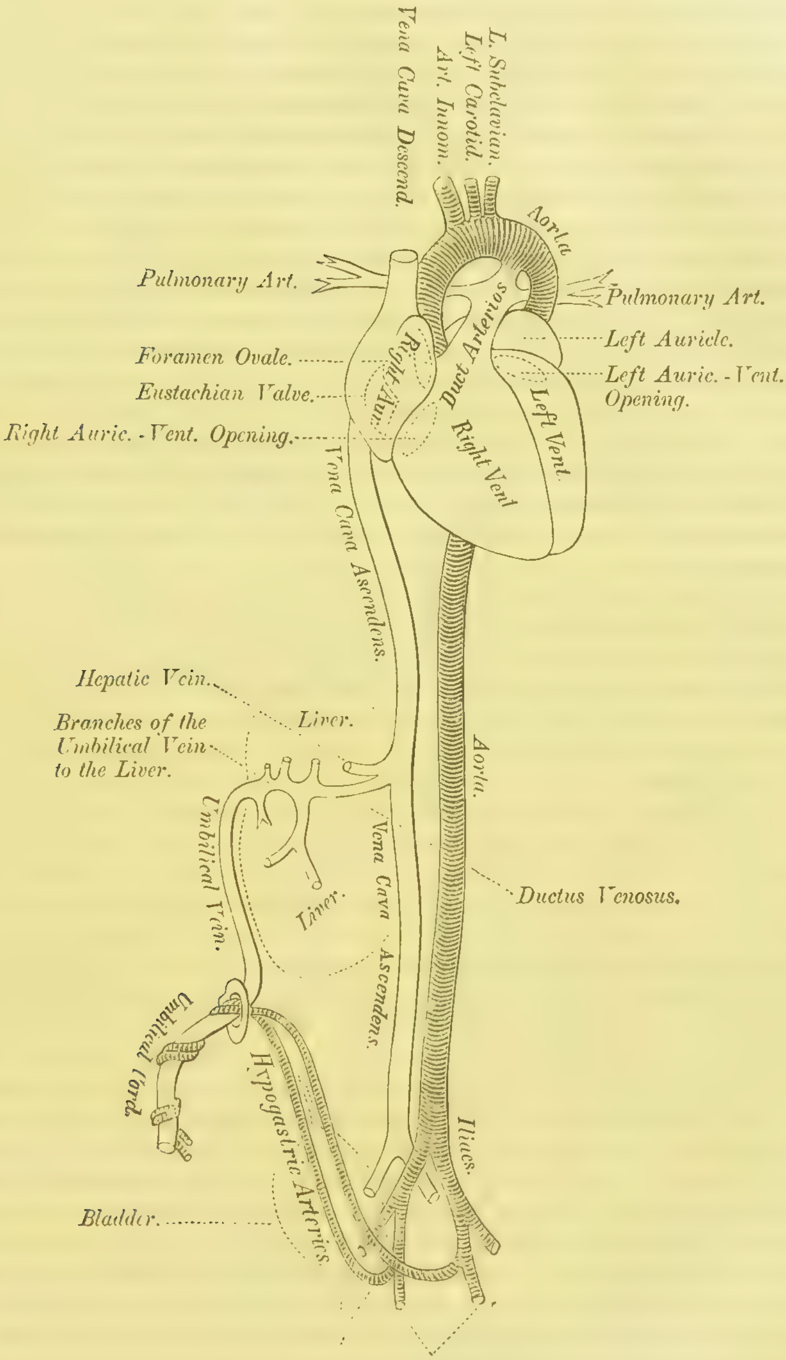
The blood poured into the left auricle from the vena cava ascendens through the foramen ovale passes from the left auricle into the left ventricle. The left auricle and the left ventricle also receive a small quantity of blood from the lungs, by the pulmonary veins. Thus the left ventricle is filled. At the same time, the right ventricle is filled with blood which has passed through the right auricle, in front of the Eustachian valve. The two ventricles, thus distended, then contract simultaneously. The blood from the right ventricle passes in small quantity to the lungs, the greater part passing through the ductus arteriosus into the descending portion of the arch of the aorta. This duct is short (half an inch in length) and about the size of a goose-quill. The blood from the left ventricle passes into the aorta and goes to the system. The vessels of the head and superior extremities being given off from the aorta before it receives the blood from the ductus arteriosus, these parts receive almost exclusively the pure blood from the vena cava ascendens, the only mixture with the placental blood being the blood from the lower extremities, the blood from the portal system, and the small amount of blood received from the lungs. After the aorta has received the blood from the ductus arteriosus, however, it is mixed blood; and it is this which supplies the trunk and lower extremities. This is one of the reasons assigned by physiologists for the greater relative development of the upper parts of the fœtus.

In Fig. 311, which is partly diagrammatic, the fœtal circulation is illustrated. In endeavoring, in this figure, to give a clear idea of the second circulation, we have not attempted to preserve the exact relations or the relative size of the organs. We have endeavored to represent, by dotted lines, the Eustachian valve, the foramen ovale, and the two auriculo-ventricular orifices. The liver, which is smaller in the diagram than it really is, and the bladder, are represented by dotted lines.

There can be no doubt that the fœtus derives materials for its nutrition and growth from the placenta, and that this also serves as a respiratory organ. In another chapter, under the head of respiration before birth, we have stated that "Legallois frequently observed a bright-red color in the blood of the umbilical vein; and, on alternately compressing and releasing the vessel, he saw the blood change in color successively from red to dark and from dark to red." This difference in color between the blood of the umbilical arteries and of the umbilical vein has, however, been denied by some authors, who state that all of the fœtal blood, while it is of nearly a uniform color, is lighter than the venous blood of the adult; but Dalton, in a direct observation upon a cat, "nearly arrived at the term of pregnancy," noted that "the difference in color between the umbilical arteries and veins was very distinct. They were both dark, but the color of the veins was very decidedly more ruddy than that of the arteries; *i. e.*, the blood in the umbilical arteries was of the color of the ordinary venous blood, while that of the umbilical veins had a color midway between the ordinary venous and arterial hues. All the fœtuses were healthy, and moved briskly after being taken out of the uterus."

There are numerous observations showing that the fœtus *in utero* makes respiratory efforts when the umbilical vessels are compressed. We believe that these, as well as the first respiration after birth, are due to a want of oxygen in the general system of the fœtus, and we think that we have demonstrated this fact by experiments. This point has already been elaborately discussed in another chapter. If our experiments and the deductions drawn from them be correct, there can be no doubt with regard to the respiratory function of the placenta, although, as far as we know, there has never been an accurate comparison of the gases contained in the blood of the umbilical arteries and the umbilical vein.

The Third, or Adult Circulation.—When the child is born, the placental circulation is suddenly arrested. After a short time, the sense of want of air becomes sufficiently intense to give rise to an inspiratory effort, and the first inspiration is made. The pulmonary organs are then, for the first time, distended with air, the pulmonary arteries



Internal Iliac Arteries.

FIG. 311.—*Diagram of the fœtal circulation.*

carry the greatest part of the blood from the right ventricle to the lungs, and a new circulation is established. During the later periods of fœtal life, the heart is gradually prepared for the new currents of blood. The foramen ovale, which is largest at the sixth month, after that time, is partly occluded by the gradual growth of a valve, which extends from below upward and from behind forward, upon the side of the left auricle. The Eustachian valve, which is also largest at the sixth month, gradually atrophies after this time, and, at full term, it has nearly disappeared. At birth, then, the Eustachian valve is practically absent; and, after pulmonary respiration becomes established, the foramen ovale has nearly closed. The arrangement of the valve of the foramen ovale is such, that, at birth, a small quantity of blood may pass from the right to the left auricle, but none can pass in the opposite direction. The situation of the Eustachian valve, on the right side of the inter-auricular septum, is marked by an oval depression, called the fossa ovalis.

As a congenital malformation, the foramen ovale may remain open, producing the condition known as cyanosis neonatorum. This may continue into adult life, and it is then attended with more or less disturbance of respiration and difficulty in maintaining the normal heat of the body. Usually, the foramen ovale is completely closed at about the tenth day after birth. The ductus arteriosus begins to contract at birth, and it is occluded, being reduced to the condition of an impervious cord, at from the third to the tenth day.

When the placental circulation is arrested at birth, the hypogastric arteries, the umbilical vein, and the ductus venosus contract, and they become impervious at from the second to the fourth day. The hypogastric arteries remain pervious at their lower portion and constitute the superior vesical arteries. A rounded cord, which is the remnant of the umbilical vein, forms the round ligament of the liver. A slender cord, the remnant of the ductus venosus, is lodged in a fissure of the liver, called the fissure of the ductus venosus.

A history of the development of the various tissues of the body belongs really to general anatomy and is usually given in works specially devoted to that subject. We have only treated of it incidentally, in our account of the development of the various organs and systems.

CHAPTER XXVIII.

FŒTAL LIFE—DEVELOPMENT AFTER BIRTH—DEATH.

Enlargement of the uterus in pregnancy—Duration of pregnancy—Size, weight, and position of the fœtus—The fœtus at different stages of intra-uterine life—Multiple pregnancy—Cause of the first contractions of the uterus in normal parturition—Involution of the uterus—Meconium—Dextral preëminence—Development after birth—Ages—Death—Cadaveric rigidity—Putrefaction.

As the development of the ovum advances, the uterus is enlarged and its walls are thickened. The form of the organ, also, gradually changes, as well as its position. Immediately after birth, its weight is about a pound and a half, while the virgin uterus weighs less than two ounces. It is a remarkable fact, demonstrated upon the living subject, by Prof. I. E. Taylor, of New York, that the neck of the uterus, while it becomes softer and more patulous during pregnancy, does not change its length, even in the very latest stages of utero-gestation. This fact is in opposition to the statements of most obstetricians, who believe that the os internum dilates, and that the neck is gradually absorbed, as it were, by the body of the uterus, during the later months of pregnancy.

We have already studied the remarkable changes which take place in the mucous membrane of the uterus during pregnancy and the mode of formation of the decidua, and we have seen that the mucous membrane of the neck does not participate in these changes and is not thrown off in parturition. The only change, indeed, which we note in the neck, aside from the softening of its texture, is the secretion of the plug of mucus which closes the os.

The changes in the walls of the uterus during pregnancy are very important. The blood-vessels become much enlarged, and the muscular fibres increase immensely in size, so that their contractions are very powerful when the fœtus is expelled.

It is evident that, on account of the progressive increase in the size of the uterus during pregnancy, it cannot remain in the cavity of the pelvis at the later months. During the first three months, however, when it is not too large for the pelvis, it sinks back into the hollow of the sacrum, the fundus being directed somewhat backward, with the neck presenting downward, forward, and a little to the left. After this time, however, the increased size of the organ causes it to extend into the abdominal cavity, so that its fundus eventually reaches the epigastric region. Its axis then has the general direction of the axis of the superior strait of the pelvis.

The enlargement of the uterus and the necessity of carrying on a greatly-increased circulation in its walls during pregnancy are attended with a temporary hypertrophy of the heart. According to Robin, it is mainly the left ventricle which is thickened during utero-gestation, and the increase in the weight of the heart at full term amounts to more than one-fifth. After delivery, the weight of the heart soon returns to nearly the normal standard.

Duration of Pregnancy.—The duration of pregnancy, dating from a fruitful intercourse, must be considered as variable, within certain limits. The method of calculation most in use by obstetricians is, to date from the end of the last menstrual period. Dr. Matthews Duncan, who has made quite a number of observations upon this point, states that the 278th day after the end of the last menses is the average day of delivery; but he admits that his method of calculation is rough, though he cannot find any that is more reliable. The observations upon which this opinion is based are the following: The day was predicted in 153 cases; in 10 cases, confinement occurred on the exact day: in 80 cases, the confinement occurred sooner, presenting an average of 7 days for each case; and, in 63 cases, the confinement occurred later, presenting an average of 8 days for each case. The great difficulty in predicting the exact time of confinement, which is very important in practice, is mainly due to the comparatively small number of reliable observations in which the pregnancy can be dated from a single intercourse or from intercourse occurring within two or three days. We have received from Prof. Fordyce Barker the following very interesting account of a case in which this observation was made in his own practice: A lady, concerning whom there could be no suspicion of inaccuracy, residing in New York, received a visit from her husband, after a long interval of absence. He arrived in this city from New Orleans, remained thirty-six hours, and then went to Europe, where he remained for four months. Exactly 298 days from the date of the first visit of the husband, the lady was confined and delivered by Prof. Barker. This occurred in 1852. Taking into account the various cases which are quoted by authors, in which conception has been supposed to follow a single coitus, there appears to be a range of variation in the duration of pregnancy of no less than 40 days, the extremes being 260 and 300 days.

In the very interesting observations of Kundrat and Engelmann, upon the changes of the uterine mucous membrane during menstruation, to which we have already referred, the idea is advanced that pregnancy dates really from a menstrual period which is prevented, as far as a discharge of blood is concerned, by fecundation of an ovum, and not from the period immediately preceding, in which the flow takes place. If we adopt this view, the changes in the mucous membrane of the uterus ordinarily terminate in a fatty degeneration of the vascular walls, which results in a capillary hæmorrhage; if, however, an ovum be fecundated, these changes do not pass into fatty degeneration, but advance to an hypertrophy, which is the first stage in the formation of the decidua. The arguments in opposition to this method of calculating the duration of pregnancy are the following: The time, with relation to the menstrual flow, at which an ovum is discharged has not been accurately determined; and it is certain that ovulation frequently does not take place until after the flow of blood has been established. This question we have fully considered in a previous chapter. It is probable, also, that intercourse is most liable to be followed by fecundation, when it occurs just after the cessation of a menstrual period, and when the female often presents unusual sexual excitement; but it is true that fecundation may follow intercourse at any time. If we admit that fecundation dates more nearly from a menstrual period prevented than from the last appearance of the flow, it would be necessary to assume that ovulation usually takes place before the flow, and fecundation would be most liable to follow intercourse occurring at that time; for we could hardly admit that an ovum, fecundated at the cessation of a menstrual period, could remain in the generative passage of the female for two or three weeks, before the mucous membrane of the uterus is prepared for its reception. These facts are so strong, that the view entertained by Kundrat and Engelmann cannot yet be adopted without reserve.

As regards the practical applications of calculations of the probable duration of pregnancy in individual cases, we must recognize the fact that the duration is variable. If we date from the end of the last menstrual period, we may adopt the average of 278 days, a little more than nine calendar months. If we adopt the view that pregnancy dates from a menstrual period which has been prevented, the duration of intra-uterine life would be about 250 days.

Size, Weight, and Position of the Fœtus.—The estimates of writers with regard to the size and weight of the embryon and fœtus at different stages of intra-uterine life present very wide variations; still, it is important to have an approximate idea, at least, upon these points, and we shall adopt the figures given by Scanzoni, as presenting fair averages. As the measurements and weights are simply approximative, the slight differences between the German and the English standards are not important. It will be useful, also, to give, as is done by Scanzoni, a review of the general development of the organs at different stages.

At the third week, the embryon is from two to three lines in length. This is about the earliest period at which measurements have been taken in the normal state.

At the seventh week, the embryon measures about nine lines. Points of ossification have appeared in the clavicle and the lower jaw; the Wolffian bodies are large; the pedicle of the umbilical vesicle is very much reduced in size; the internal organs of generation have just appeared; the liver is of large size; the lungs present several lobules.

At the eighth week, the embryon is from ten to fifteen lines in length. The lungs begin to receive a small quantity of blood from the pulmonary arteries; the external organs of generation have appeared, but it is difficult to determine the sex; the abdominal walls have closed over in front.

At the third month, the embryon is from two to two and a half inches long and weighs about one ounce. The amniotic fluid is then more abundant, in proportion to the size of the embryon, than at any other period. The umbilical cord begins to be twisted; the various glandular organs of the abdomen appear; the pupillary membrane is formed; the limitation of the placenta has become distinct. At this time, the upper part of the embryon is relatively much larger than the lower portion.

At the end of the fourth month, the embryon becomes the fœtus. It is then from four to five inches long and weighs about five ounces. The muscles begin to manifest contractility; the eyes, mouth, and nose are closed; the gall-bladder is just developed; the fontanelles and sutures are wide.

At the fifth month, the fœtus is from nine to twelve inches long and weighs from five to nine ounces. The hairs begin to appear on the head; the liver begins to secrete bile, and the meconium appears in the intestinal canal; the amnion is in contact with the chorion.

At the sixth month, the fœtus is from eleven to fourteen inches long and weighs from one and a half to two pounds. If the fœtus be delivered at this time, life may continue for a few moments; the bones of the head are ossified, but the fontanelles and sutures are still wide; the prepuce has appeared; the testicles have not descended.

At the seventh month, the fœtus is from fourteen to fifteen inches long and weighs from two to three pounds. The hairs are longer and darker; the pupillary membrane disappears, undergoing atrophy from the centre to the periphery; the relative quantity of the amniotic fluid is diminished, and the fœtus is not so free in the cavity of the uterus; the fœtus is now viable.

At the eighth month, the fœtus is from fifteen to sixteen inches long and weighs from three to four pounds. The eyelids are opened and the cornea is transparent; the pupillary membrane has disappeared; the left testicle has descended; the umbilicus is at about the middle of the body, the relative size of the lower extremities having increased.

At the ninth month, the fœtus is about seventeen inches long and weighs from five to six pounds. Both testicles have usually descended, but the tunica vaginalis still communicates with the peritoneal cavity.

At birth, the infant weighs a little more than seven pounds, the usual range being from four to ten pounds, though these limits are sometimes exceeded.

The position of the fœtus, in the great majority of cases, excluding abnormal presentations, is with the head downward; and why this is the usual and the normal position, is a question which has been the subject of much discussion. As we have just seen, in the early stages of pregnancy, the fœtus floats quite freely in the amniotic fluid. Upon this point, Dr. Matthews Duncan has made the following interesting experiments: Securing the limbs of the fœtus in the natural position which it assumes *in utero*, by means of threads, and immersing it in a solution of salt of nearly its own specific gravity, he found that it naturally gravitated to nearly the normal position, with the head downward. It is probable, judging from these observations, that the natural gravitation of the head and of the upper part of the fœtus is the determining cause of the ordinary position *in utero*.

The shape of the uterus at full term is ovoid, the lower portion being the narrower. The fœtus has the head slightly flexed upon the sternum, the arms flexed upon the chest and crossed, the spinal column curved forward, the thighs flexed upon the abdomen, the legs slightly flexed and usually crossed in front, and the feet flexed upon the legs, with their inner margin drawn toward the tibia. This is the position in which the fœtus is best adapted to the size of the uterine cavity, and in which the expulsive force of the uterus can be most favorably exerted, both as regards the fœtus and the generative passages of the mother.

Multiple Pregnancy.—It is not very rare to observe two children at a birth, and cases are on record where there have been four and even five, though in these latter instances the children generally survive but a short time, or, as is more common, abortion takes place during the first months. Three at a birth, though rare, has been often observed; and we have in mind at this moment a case of three females, triplets, all of whom lived past middle age.

In cases of twins, it is an interesting question to determine whether the development always takes place from two ova, or whether a single ovum may be developed into two beings. In the majority of cases, twins are of the same sex, though sometimes they are male and female. In some cases, there are two full sets of membranes, each fœtus having its distinct decidua, placenta, and chorion; in others, there is a single chorion and a double amnion; but, in some, both fœtuses are enclosed in the same amnion. As a rule, the two placentæ are distinct; but sometimes there is a vascular communication between them, or what appears to be a single placenta may give origin to two umbilical cords. If there be but a single chorion and amnion and a single placenta, it has been thought that the two beings are developed from a single ovum; otherwise, it would be necessary to assume that there were originally two sets of membranes, which had become fused into one. The instances on record, one of which we have given, of twins, one white and the other black, show conclusively that two ova may be developed in the uterus at the same time. While there can be no doubt upon this point, the question of the possibility of the development of two beings from a single ovum remains unsettled. It is thought to be more difficult to understand how two conjoined monsters, like the celebrated Siamese twins, who died in 1874 at the age of sixty-three years, could be developed

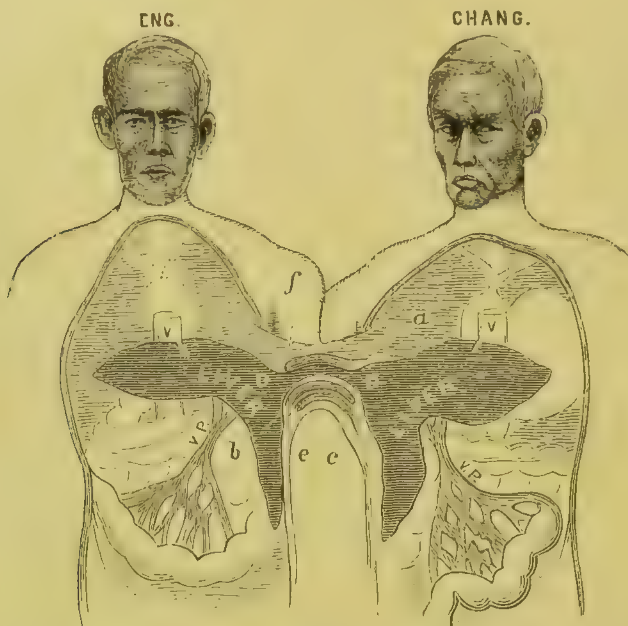


Fig. 312.—*The Siamese twins.*

V V, vena cava; V P, V P, portal vein; *a*, upper hepatic pouch of Chang; *b*, peritoneal, or umbilical pouch of Eng; *c*. lower peritoneal, or umbilical pouch of Chang; D, D, connecting liver-band; *e*, lower border of the band; *f*. upper border of the band.

from two ova which became fused, than to imagine the development of two beings from a single ovum. This question, however, belongs to teratology and could be settled only by observations of conjoined monsters very early in their development, which do not exist in literature.

As pathological conditions, we have extra-uterine pregnancies, in which the fecundated ovum, forming its attachments in the Fallopian tube (Fallopian pregnancy) or within the abdominal cavity (abdominal pregnancy), undergoes a certain degree of development. The uterus usually enlarges, in these instances, and forms an imperfect decidua.

Cause of the First Contractions of the Uterus in Normal Parturition.—The cause of the first contraction of the uterus in normal parturition is undoubtedly referable to some change in the attachment of its contents, which causes the fœtus and its membranes to act as a foreign body. When, for any reason, it is advisable to cause the uterus to expel its contents before the full term of pregnancy, the most physiological method of bringing on the contractions of this organ is to cautiously separate a portion of the membranes, as is often done by introducing an elastic catheter between the ovum and the uterine wall. A certain time after this operation, the uterus contracts to expel the ovum, which then acts as a foreign body.

In the normal state, toward the end of pregnancy, the cells of the decidua vera and of that portion of the placenta which is attached to the uterus undergo fatty degeneration, and, in this way, there is a gradual separation of the outer membrane, so that the contents of the uterus gradually lose their anatomical connection with the mother. When this change has progressed to a certain extent, the uterus begins to contract; each contraction then separates the membranes more and more, the most dependent part pressing upon the os internum; and the subsequent contractions are probably due to reflex action. The first "pain" is induced by the presence of the fœtus and its membranes as a foreign body, a mechanism similar to that which obtains when premature labor has been brought on by separation of the membranes.

We shall not describe the mechanism of parturition, although this is entirely a physiological process, for the reason that it is necessarily considered elaborately in works upon obstetrics. The first contractions of the uterus, by pressing the bag of waters against the os internum, gradually dilate the cervix; the membranes usually rupture when the os is pretty fully dilated, and the amniotic fluid is discharged; the head then presses upon the outlet; and, the uterine contractions becoming more and more vigorous and efficient, the child is brought into the world, this being followed by the expulsion of the membranes and placenta. There then follows a tonic contraction of the muscular walls of the uterus, which becomes a hard, globular mass, easily felt through the flaccid abdominal walls. The very contractions of the muscular fibres of the uterus which expel the fœtus close the vessels ruptured by the separation of the placenta and arrest the hæmorrhage from the mother. The changes which then take place in the respiration and the circulation of the infant have been fully considered in connection with the development of the circulatory system.

Involution of the Uterus.—At from four to six days, and seldom later than eight days after parturition, the uterus has sensibly advanced in the process of involution; and it is then gradually reduced to the size and structure which it presents during the non-pregnant condition, though it never becomes quite as small as in the virgin state. The new mucous membrane, which has been developing during the latest periods of pregnancy, becomes perfect at about the end of the second month after delivery. It has then united, at the os internum, with the mucous membrane of the neck, which does not participate in the formation of the decidua. The muscular fibres, after parturition, present granules and globules of fat in their substance, and are gradually reduced in size, as the uterus becomes smaller. Their involution is complete at about the end of the second month. During the first month, and particularly within the first two weeks after delivery, there is a sero-sanguinolent discharge from the uterus, which is due to disintegration of the blood and of the remains of the membranes in its cavity, this *débris* being mixed with a certain amount of sero-mucous secretion. This discharge constitutes the lochia, which are at first red, but become paler as they are reduced in quantity and disappear.

During lactation, the processes of ovulation and menstruation are usully arrested, though this is not always the case. In treating of secretion, we have given a full description of the vernix caseosa, and we have also stated what is known with regard to the properties and composition of the urine of the fœtus.

Meconium.—At about the fifth month, there appears a certain amount of secretion in the intestinal canal, which becomes more abundant, particularly in the large intestine, as development advances. This is rather light-colored or grayish in the upper portion of the small intestine, becoming yellowish in the lower portion, and is of a dark-greenish color in the colon. The dark, pasty, adhesive matter, which is discharged from the rectum soon after birth, is called the meconium.

The meconium appears to consist of a thick, mucous secretion, with numerous grayish granules, a few fatty granules, intestinal epithelium, and, frequently, crystals of cholesterine. The color seems to be due to granulations of the coloring matter of the bile, but the biliary salts cannot be detected in the meconium by Pettenkofer's test. The constituent of the meconium which, in our own observations, we have found to possess the greatest physiological importance, is cholesterine. Although but few crystals of cholesterine are found upon microscopical examination, the simplest processes for its extraction will reveal the presence of this principle in large quantity. In a specimen of meconium in which we made a quantitative examination, the proportion of cholesterine was 6·245 parts per 1,000. It is a significant fact, that the meconium contains cholesterine and no stercorine, the stercorine, in the adult, resulting from a transformation of cholesterine by the digestive fluids, which are probably not secreted during intra-uterine life.

FIG. 313.—*Cholesterine extracted from meconium; $\frac{1}{10}$ inch objective.*

None of the secretions concerned in digestion appear to be produced *in utero*, and it is also probable that the true biliary salts are not formed at that time; but we know that the processes of disassimilation and excretion are then active, and the cholesterine of the meconium is the product of the excretory action of the liver. The relations of cholesterine as an excrementitious principle have already been very fully discussed, in connection with the bile and with excretion.

Dextral Preëminence.—The curious fact, that most persons by preference use the right arm, leg, eye, etc., instead of the left, while, as exceptions, some use the left in preference to the right, has excited a great deal of discussion, even among the earlier writers. There can be no doubt with regard to the fact of a natural dextral preëminence; and, also, that left-handedness is congenital, difficult, if not impossible, to correct entirely, and not due simply to habit. It would appear that there must be some condition of organization, which produces dextral preëminence in the great majority of persons, and left-handedness, as an exception; but what this condition is, it is very difficult to determine. An explanation, very often offered by anatomists, is, that the right subclavian artery arises nearer the heart than the left, that the right arm is therefore better supplied with arterial blood, develops more fully, and is, consequently, generally used in preference to the left; but we cannot explain the exceptional predominance of the left hand by an inversion of this arrangement of vessels.

The most important anatomical and pathological facts bearing upon the question under consideration are the following: Dr. Boyd has shown that the left side of the brain almost invariably exceeds the right in weight, by about one-eighth of an ounce. In aphasia, the lesion is almost always on the left side of the brain. These facts point to a predominance of the left side of the brain, which presides over the movements of the right side of the body. Again, a few cases of aphasia with left hemiplegia, the lesion being on the right side of the brain, have been reported as occurring in left-handed persons. These points we have noted in treating of the nervous system.

Dr. Ogle, in a recent paper on right-handedness, gives several instances of aphasia in left-handed persons, in which the brain-lesion was on the right side. In two left-handed individuals, the brain was examined and compared with the brain of right-handed persons. It was found that the brain was more complex on the left side in the right-handed, and on the right side in the left-handed. In the discussion which followed the presentation of this paper, Dr. Charlton Bastian stated that he had found the gray matter of the brain to be generally heavier on the left than on the right side. With regard to the cause of the superior development of the left side of the brain, the only explanation offered was the fact that the arteries going to the left side are usually larger than those on the right. There were no observations with regard to the comparative size of the arteries upon the two sides in left-handed persons.

Reasoning from the facts just stated, Dr. Ogle conceives that dextral preëminence depends upon a natural predominance of the left side of the brain, the reverse obtaining in the left-handed. This view seems to afford the most rational explanation of dextral preëminence. It is generally true that the members on the right side are stronger than the left, particularly the arm; but this is not always the case, even in the right-handed. A not inconsiderable practical experience in athletic exercises has led us to observe that the right hand is more conveniently and easily used than the left, from which fact we derive the term dexterity; but that the left arm is often stronger than the right. In many feats of strength, the left arm appears less powerful than the right, because we have less command over the muscles. As a single illustration of this, we may mention the feat of drawing the body up with one arm, which requires unusual strength, but very little dexterity. In a number of right-handed persons, we find many who perform this feat more easily with the left arm, and not a few who can accomplish it with the left arm and not with the right. When we come to the cause of the superior development of the left side of the brain, we must confess that the anatomical explanation is not entirely satisfactory. We can only say that the two sides of the brain are generally not exactly equal in their development, the left side being usually superior to the right, and that we ordinarily use the muscles of the right side of the body in preference to those of the left side.

Development after Birth, Ages, and Death.

When the child is born, the organs of special sense and the intelligence are dull; there is then very little muscular power; and the new being, for several weeks, does little more than eat and sleep. The natural food at this time is the milk of the mother, and the digestive fluids do not, for some time, possess the varied solvent properties that we find in the adult, though observations upon the secretions of the infant are few and rather unsatisfactory. The full activity of pulmonary respiration is gradually and slowly established. Young animals appropriate a comparatively small quantity of oxygen, and, just after birth, they present a much greater power of resistance to asphyxia than the adult. The power of maintaining the animal temperature is also much less in the newly-born. The process of ossification, development of the teeth, etc., have already been considered. The hairs are shed and replaced by a new growth a short time after birth. The fontanelles gradually diminish in size after birth, and they are completely closed at the age of about four years.

The period of life which dates from birth to the age of two years is called infancy At the age of two years, the transition takes place from infancy to childhood. The child is now able to walk without assistance, the food is more varied, and the digestive operations are more complex. The special senses and the intelligence become more acute, and the being begins to learn how to express ideas in language. The child gradually develops, and the milk-teeth are replaced by the permanent teeth. At puberty, which begins at from the fourteenth to the seventeenth year—a little earlier in the female—the development of the generative organs is attended with important physical and moral changes.

The different ages recognized by the older writers were as follows: Infancy, from birth to the age of five years; adolescence, or youth, to the twenty-fifth year; adult age, to the thirty-fifth year; middle life, to the fiftieth year; old age, to the sixtieth year; and then, extreme old age. A man may be regarded at his maximum of intellectual and physical development at about the age of thirty-five, and he begins to decline after the sixtieth year, although such a rule, as regards intellectual vigor, would certainly meet with numerous exceptions.

We do not propose to consider, in this connection, the psychological variations which occur at different ages, but, as regards the general process of nutrition, it may be stated, in general terms, that the appropriation of new matter is a little superior to disassimilation up to about the age of twenty-five years; between twenty-five and forty-five, these two processes are nearly equal; and, at a later period, the nutrition does not completely supply the physiological waste of the tissues, the proportion of organic to inorganic matter gradually diminishes, and death follows, as an inevitable consequence of life. In old age, the muscular movements gradually become feeble; the bones contain an excess of inorganic matter; the ligaments become stiff; the special senses are usually obtuse; and there is a diminished capacity for mental labor, with more or less loss of the memory and of intellectual vigor. It is a curious fact that remote events are more clearly and easily recalled to the mind in old age, than those of recent occurrence; and, indeed, early impressions and prejudices then appear to be unusually strong.

It frequently happens, in old age, that some organ essential to life gives way, and that this is the immediate cause of death; or that an old person is stricken down by some disease to which his age renders him peculiarly liable. It is so infrequent to observe a perfectly physiological life, continuing throughout the successive ages of man, that it is almost impossible to present a picture of physiological death; but we sometimes observe a gradual fading away of vitality in old persons, who die without being affected with any special disease. It is also difficult to fix the natural period of human life. Some persons die, apparently of old age, at seventy, and it is rare that life is preserved beyond one hundred years. In treating of the so-called vital point, we have stated that there does not seem to be any such occurrence, except under conditions of most extraordinary external violence, as instantaneous death of all parts of the organism. If we confine ourselves to physiological facts, we cannot admit the existence of a single vital principle which animates the entire organism. Each tissue appears to have its peculiar property, dependent upon its exact physiological constitution, which we call vitality; a term which really explains nothing. The tissues usually die successively, and not simultaneously, nearly all of them being dependent upon the circulating, oxygen-carrying blood for the maintenance of their physiological properties. It has been demonstrated, indeed, that the so-called vital properties of tissues may be restored, after apparent death, by the injection of blood into their vessels.

After death, there is often a discharge of the contents of the rectum and bladder, and parturition, even, has been known to take place. The appearance which indicates growth of the beard after death is probably due to shrinking of the skin and, perhaps, contraction of the smooth muscular fibres attached to the hair-follicles. The most important phenomenon, however, which is observed before putrefaction begins, is a general rigidity of the muscular system.

Cadaveric Rigidity.—At a variable period after death, ranging usually from five to seven hours, all of the muscles of the body, involuntary as well as voluntary, become rigid and can only be stretched by the application of considerable force. Sometimes, especially after long-continued and exhausting diseases, this rigidity appears as soon as a quarter of an hour after death. In the case of persons killed suddenly, while in full health, it may not be developed until twenty or thirty hours after death, and it then continues for six or seven days. Its average duration is from twenty-four to thirty-six hours; and, as a rule, it is more marked and lasts longer, the later it appears. In warm weather, cadaveric rigidity appears early and continues for a short time. When the contraction is overcome by force, after the rigidity has been completely established and has continued for some time, it does not reappear. The rigidity of the muscular system extends to the muscular coats of the arteries and the lymphatics. It is for this reason that the arterial system is usually found empty after death. The rigidity first appears in the muscles which move the lower jaw; then it is noted in the muscles of the trunk and neck, extends to the arms, and finally, to the legs, disappearing in the same order of succession. The stiffening of the muscles is due to a sort of coagulation of their substance, analogous to the coagulation of the blood, and is probably attended with some shortening of the fibres; at all events, the fingers and thumbs are generally flexed. That the rigidity is not due to coagulation of the blood, is shown by the fact that it occurs in animals killed by hæmorrhage.

According to John Hunter, the blood does not coagulate nor do the muscles become rigid in animals killed by lightning or hunted to death; but it is a question, in these instances, whether the rigidity does not begin very soon after death and continue for a brief period, so that it may escape observation. As a rule, rigidity is less marked in very old and in very young persons than in the adult. It occurs in paralyzed muscles, provided they have not undergone extensive fatty degeneration.

Under ordinary conditions of heat and moisture, as the rigidity of the muscular system disappears, the processes of putrefaction commence. The various tissues, with the exception of certain parts, such as the bones and teeth, which contain a large proportion of inorganic matter, gradually decompose, forming water, carbonic acid, ammonia, etc., which pass into the earth and the atmosphere. The products of decomposition of the organism are then in a condition in which they may be appropriated by the vegetable kingdom.

INDEX.

THE END.